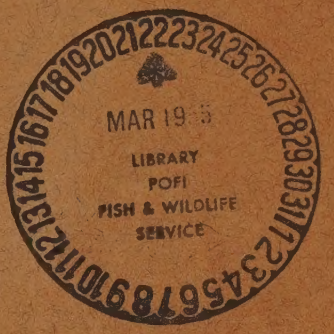
B1
V.8
Pt 1

B.A.N.Z.
ANTARCTIC RESEARCH EXPEDITION
1929-1931

UNDER THE COMMAND OF SIR DOUGLAS MAWSON, Kt., O.B.E., B.E., D.Sc., F.R.S.

REPORTS—SERIES B (Zoology and Botany)



VOLUME VIII

PART 1

TAXONOMY, DISTRIBUTION AND DEVELOPMENT OF THE EUPHAUSIACEA (CRUSTACEA)

By

KEITH SHEARD

ADELAIDE
PUBLISHED BY THE B.A.N.Z.A.R. EXPEDITION COMMITTEE
and issued through the Barr Smith Library, University of Adelaide
Printed at The Hassell Press
30th June, 1953
Price thirty-two shillings sterling (post free)

ALL RIGHTS RESERVED

Wholly set up and printed in Australia, at The Hassell Press, Adelaide
Registered at the General Post Office, Adelaide, for transmission through the post as a book

REPORTS OF B.A.N.Z. ANTARCTIC RESEARCH EXPEDITION, 1929-1931

SERIES A.

			s.	d.
			sterling (post free)	
Vol. I.		Geographical Report (in preparation)		
Vol. II	Part 1.	Rocks from Enderby Land. *By C. E. Tilley*	4	0
	Part 2.	Rocks from MacRobertson Land. *By C. E. Tilley*		
	Part 3.	The Petrology of Heard Island. *By G. W. Tyrrell*	5	0
	Part 4.	The Petrology of Possession Island (Crozets). *By G. W. Tyrrell*		
	Part 5.	The Tertiary Lavas of Kerguelen Island. *By A. B. Edwards*	5	0
	Part 6.	Marine Tertiary Fossils from Kerguelen Island. *By H. O. Fletcher*	3	0
	Part 7.	Soils from Subantarctic Islands. *By C. S. Piper*	2	0
	Part 8.	Plant Microfossils from the Lignites of Kerguelen Archipelago, *By Isabel C. Cookson*	4	6
Vol. III.	Part 1.	Soundings, *by S. A. C. Campbell; M. H. Moyes; K. E. Oom, and the Ship's Officers*	3	6
	Part 2.	Hydrology. *By A. Howard and H. V. Sverdrup*	11	6
Vol. IV.	Part 1.	Terrestrial Magnetism. *By C. Coleridge Farr*	3	6
	Part 2.	Meteorology (in preparation).		

Other Reports, including Glaciology, are also in preparation.

SERIES B.

Vol. I.	Part 1.	Biological Organization and Station List. *By T. Harvey Johnston* (1937)	5	6
	Part 2.	Fishes. *By J. R. Norman* (1937)	5	0
	Part 3.	Cephalodiscus. *By T. Harvey Johnston and Nancy G. Muirhead* (1951)	10	0
Vol. II.		Birds. *By R. A. Falla* (1937)	50	0
Vol. III.		Reports on Mammals (in preparation)		

(Continued on inside back cover)

Exped. Repts
Q115
B1
V.8
pt.1
not rec'd

PART 1

TAXONOMY, DISTRIBUTION AND DEVELOPMENT OF THE EUPHAUSIACEA (CRUSTACEA)

By

KEITH SHEARD

[B.A.N.Z.A.R.E. REPORTS, Series B, Vol. VIII, Part 1, Pages 1-72, Tables 1-17; Text Figures 1-17]

Issued 30th June, 1953

CONTENTS

PAGE

A. INTRODUCTION - - - - - - - - - - - - - - - 5

B. SOURCES OF MATERIAL - - - - - - - - - - - - - 5

C. THE ROLE OF THE EUPHAUSIACEA IN THE MARINE ECONOMY - 5

D. A SYNOPSIS OF THE ORDER EUPHAUSIACEA - - - - - - - 7

1. THE FAMILIES OF THE EUPHAUSIACEA - - - - - - - - - - 7

2. THE GENERA AND SPECIES OF THE EUPHAUSIACEA - - - - - - 8

(a) A sorting key to the genera - - - - - - - - - - 8

(b) Generic diagnoses and working keys to the species - - - - - 9

(i) The genus *Thysanopoda* - - - - - - - - - - 9

(ii) „ „ *Meganyctiphanes* - - - - - - - - - - 11

(iii) „ „ *Nyctiphanes* - - - - - - - - - - - 11

(iv) „ „ *Pseudeuphausia* - - - - - - - - - - 12

(v) „ „ *Euphausia* - - - - - - - - - - - 12

(vi) „ „ *Thysanoessa* - - - - - - - - - - - 16

(vii) „ „ *Tessarabrachion* - - - - - - - - - - 18

(viii) „ „ *Nematoscelis* - - - - - - - - - - 18

(ix) „ „ *Nematobrachion* - - - - - - - - - - 19

(x) „ „ *Stylocheiron* - - - - - - - - - - 20

E. THE DISTRIBUTION OF THE EUPHAUSIACEA - - - - - - - 21

1. GENERAL DISTRIBUTION - - - - - - - - - - - - - 21

2. EUPHAUSIACEA OF THE B.A.N.Z.A.R.E. STATIONS - - - - - - - 26

3. EUPHAUSIACEA OF THE WESTERN SOUTH PACIFIC - - - - - - - 27

(a) South-Eastern Australian "Warreen" Stations - - - - - - 27

(b) R.R.S. "Discovery II" traverses, October, 1950 - - - - - 29

(c) Distribution and Temperature - - - - - - - - - - 29

(d) Euphausiacea of the Eastern Australian Continental Shelf - - - 30

(e) Oceanic distribution, Lat. 15° S. to 65° S. - - - - - - - - 30

(f) Corrections to Oceanographical Station Lists - - - - - - - 33

(g) Layering and vertical movements of the Euphausiacea - - - - 33

F. DIFFERENTIATION, DEVELOPMENT AND GROWTH IN THE EUPHAUSIACEA - - - - - - - - - - - - - - - - - - 33

1. DIFFERENTIATION AND DEVELOPMENT - - - - - - - - - - 34

(a) Historical - - - - - - - - - - - - - - - 34

(i) Descriptions of larval development - - - - - - - - 34

(ii) Theories of development - - - - - - - - - - - 34

(iii) The use of the term "dominant" - - - - - - - - - 35

2. LARVAL DEVELOPMENT OF SELECTED SPECIES - - - - - - - - 36

(a) Method - - - - - - - - - - - - - - - 36

(b) Nomenclature - - - - - - - - - - - - - - 36

(c) Identification of *Nyctiphanes australis*, etc. - - - - - - - 38

(d) The larval development of *Nyctiphanes australis* - - - - - - 40

(i) Instar sequences - - - - - - - - - - - - 40

(ii) Monthly occurrences of larval instars - - - - - - - - 46

2. Larval development of selected species — Page

(e) The larval development of *Euphausia recurva* - - - - - - - 46

(f) Larvae of *Euphausia similis* - - - - - - - - - - - - 46

(g) The larvae of *Euphausia spinifera* - - - - - - - - - - 46

(h) The larvae of *Pseudeuphausia latifrons* - - - - - - - - 47

(i) The larvae of *Thysanoessa gregaria* - - - - - - - - - 47

(j) The larvae of *Nematoscelis difficilis* - - - - - - - - - 48

3. Growth, relative growth and change of form - - - - - - - - 48

(a) Historical - - - - - - - - - - - - - - - - 48

(b) Relative growth in *Nyctiphanes australis* - - - - - - - - 49

(c) Change in body proportions of *Nyctiphanes australis* - - - - - - 52

4. Function, form, development and growth in the Euphausiacea - - - - 55

(a) Function - - - - - - - - - - - - - - - - 55

(b) Form - - - - - - - - - - - - - - - - - 55

(c) Development and growth - - - - - - - - - - - - 55

5. The furcilia phases in the Euphausiacea - - - - - - - - - 56

G. ACKNOWLEDGMENTS - - - - - - - - - - - - - - - 60

H. APPENDIX - - - - - - - - - - - - - - - - - 61

I. BIBLIOGRAPHY - - - - - - - - - - - - - - - - 70

1. Euphausiacea, Biology - - - - - - - - - - - - - 70

2. Growth - - - - - - - - - - - - - - - - - 71

3. Euphausiacea, Palaeontology - - - - - - - - - - - - 72

TAXONOMY, DISTRIBUTION AND DEVELOPMENT OF THE EUPHAUSIACEA (CRUSTACEA)*

by KEITH SHEARD.†

(Tables 1-17, Figs. 1-17.)

A. Introduction.

The Euphausiacea are of considerable importance in the marine economy. This report aims at providing a working synopsis of the species, an account of their general distribution, and an analysis of growth and development in certain species, notably in *Nyctiphanes australis* Sars. As a result of that analysis a progressive nomenclature has been suggested for the furcilia instars, while the furcilia phase has been divided into three stages.

In addition to a bibliography of the taxonomy and distribution of the species of the order a list of the relevant literature on growth and relative growth has been provided.

B. Sources of Material.

Systematic traverses for the collection of plankton, and of hydrological data in south-eastern Australian coastal and slope waters extending approximately from 26° south Latitude to 44° S. were commenced in 1938 when the Fisheries Research Vessel "Warreen" was commissioned by the Division of Fisheries, Council of Scientific and Industrial Research (later the Commonwealth Scientific and Industrial Research Organization). These concluded in 1942 when the vessel was transferred to naval duty as H.M.A.S. "Stella." A study of the crustacean components of the zooplankton was commenced in 1939. Later, as detailed in part 1 of this series (Sheard, 1947) it became possible to include in the study the Antarctic and Sub-antarctic plankton of the B.A.N.Z. Antarctic Research Expedition (1929-31). This plankton material was supplemented by that collected over the period 1942 to 1950 in New South Wales, South Australian, and Western Australian waters by the writer in order to examine various aspects of the problem of Euphausiid distribution and development. R.R.S. "Discovery II" carried out two off-shore traverses in the New South Wales area in October, 1950, for the Division of Fisheries, C.S.I.R.O., and the results of these have been summarized in this report.

The collections totalled 2,741 samples obtained from plankton tows at levels ranging from the surface to 1,000 metres, using Discovery type N 70, N 100, and N 200 nets. They contained representatives of all the planktonic crustacean orders; and of the Euphausiacea 49 out of the 86 known species. Since the neritic species *Nyctiphanes australis* G. O. Sars was present in many samples in large swarms, including its readily identifiable larval stages, a detailed study was planned on the distribution and development of that species. Other sub-tropical species, e.g. *Euphausia recurva* Hansen, *Euphausia spinifera* Sars, *Nematoscelis difficilis* Hansen and *Thysanoessa gregaria* Sars were treated in less detail.

In view of the intensive studies of the Antarctic Euphausiacea in the Discovery Reports, and of the very large amount of such material now undergoing analysis by British workers as a result of the recent circumpolar cruise of "Discovery II" it has been considered reasonable to restrict detailed comment on the B.A.N.Z.A.R.E. Antarctic Euphausiacea to a minimum. Reports on other elements of the Antarctic plankton taken during the B.A.N.Z.A.R.E. traverses will be issued in later parts of this series.

C. The Role of the Euphausiacea in the Marine Economy.

While it was recognised in the early stages of the study of the food relationships of marine animals that the Copepoda were prime converters of phytoplankton, representing an important constituent of the food chain of many fishes (particularly the Clupeoidea), this recognition has been slower to develop in the case of the Euphausiacea. This has been due, in part to the members of this order not being such obvious features of the plankton, and in part to the relative ease of capture of Copepoda by standard plankton nets. Except for periods of surface swarming, neritic Euphausiids are inhabitants of the detrital bearing, near-bottom water layers of the continental shelves and their associated banks (i.e. of the commercial trawl zone), in which water layers sampling is difficult. Hickling (1924), following Holt and Tattersall (1905), demonstrated however that adequate sampling there was possible by attaching small plankton nets to the headline of fishing

*Contribution No. 129 from the Marine Biological Laboratory, C.S.I.R.O., Division of Fisheries, Cronulla, New South Wales.

†An officer of C.S.I.R.O., Division of Fisheries, stationed at Department of Biology, University of Western Australia.

trawls. In Australian waters I have used such small nets attached to the spreader bar of Danish Seines with equal success.

Einarsson (1945) has summarised the role of the Euphausiacea in the food chains of animals principally of the North Atlantic; the northern species of the Euphausiidae referred to include *Thysanoessa longicaudata, T. raschii, T. inermis, Meganyctiphanes norvegica* (a slope species) and *Nyctiphanes couchii* (a neritic species); the southern species include *Euphausia superba,* the importance of which in the economy of whales in the Antarctic is well known. Even in the North Atlantic and North Sea, where important commercial fish species such as the cod and herring show considerable dependence on the production and distribution of Euphausiacean species, there has been little continuous study of the stomach contents of the fishes concerned, although the importance of such studies with regard to the variations in distribution, alterations in habit, and fluctuations in numbers, of commercial fish species is indisputable.

During the course of the present investigations in Australian seas such continuous studies were not made; but fish stomach contents were examined from time to time. Crustacean remains were a common constituent of this material. It was obvious that schooling aggregation and behaviour, for feeding purposes, of many fish species depended, at first or second remove, on the swarming of crustacean species for breeding purposes, as well as on swarms of their larvae, either as they became concentrated in local rips and eddies, or as they were released in floods during brief, mass hatching periods. Crustacea which swarm during their breeding period, and which were common in fish stomachs, included such species as *Nyctiphanes australis, Euphausia recurva* and *Thysanoessa gregaria* among the Euphausiacea; *Calanus* spp., *Acartia clausii* and *Temora* spp. among the Copepoda and *Euthemisto australis* among the Hyperiid Amphipoda. Euphausiacean species with large larval swarms included *N. australis, T. gregaria, E. recurva, E. spinifera, Nematoscelis difficilis,* and *Pseudeuphausia latifrons.*

In neritic waters it was apparent that a considerable number of species of commercial fishes congregated to a greater or lesser extent on concentrations of adult and larval phases of *N. australis.* These included the following species: The southern bluefin tuna *(Thunnus maccoyii),* the striped tuna *(Katsuwonus pelamis),* the barracoota *(Thyrsites atun),* the Australian pilchard *(Sardinops neopilchardus),* and the tiger flathead *(Neoplatycephalus macrodon).* The latter species, normally a trawl-zone feeder, whose stomach contents in that phase often contained large quantities of bottom feeding *N. australis,* was often taken in mid-water during September and October crammed with adult *N. australis* with ripe gonads.

It was noteworthy also that the vast breeding aggregations of the Tasmanian mutton bird *(Puffinus tenuirostris)* in Bass Strait during the period October to April appeared to be dependent largely on *N. australis* and *T. gregaria,* and, to a lesser degree on the Hyperiid Amphipod *(Euthemisto australis).*

The food sources of the Euphausiacea themselves appeared to be two-fold. Some species were direct feeders on phytoplankton and the associated small zooplankton, and some exploited detrital layers, often those lying immediately above the sea-bottom, together with the smaller, associated zooplankton. One and the same species, e.g. *N. australis,* played both roles, although, even in that case, the species may have been acting somewhat as a detrital feeder in relation to the phytoplankton and its accompanying zooplankton. This was indicated during a brief but very intense period of flowering of the diatom, *Stephanopyxis turris,* with which was associated the copepod, *Calanus finmarchicus,* in the Ulladulla region of New South Wales during September 1944, when many specimens of *N. australis* were taken with their "food baskets" chiefly filled with copepod, faecal pellets, with fresh diatoms at a minimum. Simultaneous, staged vertical N 70 net hauls indicated by difference that *Nyctiphanes australis* was in its maximum concentration below the strata of copepods and diatoms at 20 to 30 metres (the maximum concentration of copepods lying at about 10 metres, in the diatom mass, but below its major concentration).

This observation suggested a detailed investigation of the Euphausiacea from the oblique and vertical hauls of the B.A.N.Z. Antarctic Research Expedition and, although the number of samples containing Euphausiids was limited, it was found that in the majority of specimens from each haul the chief constituents of the food baskets were faecal pellets. This occurred in spite of the fact that the specimens were in bottles which contained as their major constituent fresh diatoms. The Euphausiacean species involved were *Euphausia superba, E. triacantha, E. spinifera, E. similis, Thysanoessa macrura* and *T. vicina.* Confirmation is required from larger sources of material (e.g. that of the "Discovery" cruises), but it is possible that a prime food source of species of the Euphausiacea in areas of high diatom production may well be the faecal material of the grazing herbivores. In the poorer Australian waters only one case of Euphausiid *(N. australis)* feeding in association with copepods *(Calanus finmarchicus)* on a diatom complex was found. This was at Eden, New South Wales, in October 1943. In this case about equal numbers of *Nyctiphanes* contained fresh diatoms *(Chaetoceros spp.)* in their food baskets as contained faecal pellets. Series of vertical hauls were made, and these indicated, by difference, that those specimens containing faecal pellets were feeding below the main copepod-diatom mass, which extended to a depth of between 10 and 15 metres.

It can thus be appreciated that the Euphausiacea, particularly the known detrital feeders, e.g. species of the genus *Nyctiphanes,* are important from the point of view of commercial fisheries in that they present a means of returning nutrient material which has been organized in the primary pelagic cycle, but which has passed beyond the reach of the carnivorous fishes, directly into their part of the cycle again. In addition, through the conversion of detrital matter resulting from the activities of bottom living organisms, such Euphausiids provide a means of introducing organic material resulting from the secondary bottom cycle into the primary

pelagic cycle, in a form directly usable by the pelagic carnivores. (This latter occurs also through the release of larvae of bottom living organisms into the pelagial.)

The existence of these two sets of transferring agents would suggest that estimates of marine productivity (in terms of fishery production) based on the conventional conversion and regeneration cycle of nutrients may be underestimated, particularly in warmer, shallow seas. Accordingly the Euphausiacea may be regarded as filling two roles in the pelagic productivity pyramid. The first being that of intercepting organic nutrient material in its journey through the breakdown phase of the cycle, and of returning it directly to the carnivore population. The second (together with the pelagic larvae of bottom-living invertebrates) being that of delivering some products of the bottom cycle of organic production to the pelagic cycle.

Some explanation of the apparent excess of production of carnivores, when measured against primary nutrient values and phytoplankton production in sub-tropical and tropical seas, may lie in this dual buffer and transference role of the Euphausiacea.

D. A Synopsis of the Order Euphausiacea.

The Order Euphausiacea (class, Crustacea; sub-class, Malacostraca; division, Eumalocatraca; series, Eucarida) comprises two families and eleven genera. Some 86 taxonomic species are recognised but several of these are ill-defined and doubtful.

Pioneer workers in monographing the Euphausiacea were G. O. Sars (1885) and H. J. Hansen (1905-1916). Subsequently, as the importance of the members of the order in relation to the cycle of organic matter in the sea, began to be appreciated, and as oceanographic expeditions multiplied, a considerable body of literature developed. Regional monographs such as those of Tattersall (1924-1939), John (1936), Einarsson (1945), and Banner (1950), have added greatly to the knowledge of the classification of the species, but no recent taxonomic conspectus exists. The present section is not intended as a taxonomic review but as a set of keys and synopses to aid in the sorting of Euphausiid material preliminary to its more precise treatment.

> Accordingly the definitions of families and genera are given in detail; but the treatment of the species is not extended beyond the provision of working keys, except in some cases descriptions of the petasma, the male copulatory organ are provided. The species sections are not intended as a substitute for the detailed descriptions given by the original authors and redescribers of the species. Synonomy and references have been reduced to the minimum required to lead back ultimately to first descriptions and to important emendments. The species themselves are figured sufficiently well in the references for the terminology used in the keys to be worked out readily, by comparison, in the usual manner.

Great care must be exercised in the identification of immature specimens when using species descriptions based on adults, as the definitive form is often reached only in late adolescence. In consequence, synonomy is cluttered with species mistakenly erected as the result of the mis-identification of post-larval and adolescent forms. Hansen's recognition of the importance of the male copulatory organ, the petasma; and Einarsson of that of the receptor organ, the thylecum, in the female, have reduced the possibility of error with regard to the adults. Little yet is known of the variability in the petasma while the examination of the thylecum presents some difficulties, as the structure is often obscured on the sternum.

In the main, each species possesses a characteristic body form (the *habitus* of earlier taxonomists), the resultant of a large number of small characters, few of which can be isolated. For example, in the genus *Thysanopoda,* species belonging to Section 1 of group A may be separated from those of Section 2 of that group at sight, after some acquaintance with the species; yet it is difficult to find any obvious taxonomic character for separation, other than the presence or absence of a small lateral denticle on the lower margin of the carapace.

The groupings followed in the following keys are taxonomic, i.e. they are classifications of convenience, and do not imply necessary relations or evolutionary trends, except where this is indicated by the use of the term "natural group," following the example of John (1936).

The thoracic appendages possible are reckoned as numbering eight, commencing with the pediform maxilliped as thoracic limb 1, and so on, posteriorly. *Bentheuphausia* is the only genus in which all eight pairs of thoracic limbs are fully formed. In all other genera the eighth, or the seventh and the eighth are rudimentary.

1. THE FAMILIES OF THE EUPHAUSIACEA.

Order EUPHAUSIACEA.

Malacostraca, series Eucarida, with carapace firmly connected dorsally with all the thoracic segments, leaving only part of the last segment as such, exposed dorsally. Paired eyes, on movable stalks, generally well developed. Maxillipeds (first thoracic limb), elongate, pediform with the exopod well developed natatory, the epipod rudimentary or lacking.

The eighth, or seventh and eighth thoracic limb rudimentary *(Euphausiidae),* or complete *(Bentheuphausiidae).* Exopods present on all fully developed limbs; gills present on the coxa of thoracic limb 2 to 8. Gills not covered by the carapace. Oostegites not present but secreted ovisacs occur in some genera *(Nyctiphanes, Pseudeuphausia, Nematoscelis, Stylocheiron),* carried beneath the posterior part of the thorax. Complex thoracic and abdominal luminescent organs (photophores) present in the *Euphausiidae,* absent in the *Bentheuphausiidae.* First two pairs of pleopoda modified as copulatory organs in the male *(Euphausiidae),* not modified

(Bentheuphausiidae). A spermatheca (thylecum) exists in the females of the Bentheuphausiidae, and in most genera (*Nyctiphanes,* certainly an exception) of the *Euphausiidae,* situated ventrally on the sixth thoracic segment.

Young hatch as nauplii or meta-nauplii and pass through a series of larval stages.

The order is marine, pelagic, in all oceans.

Two families, Bentheuphausiidae and Euphausiidae, are now recognised.

FAMILY BENTHEUPHAUSIIDAE COLOSI 1917.

In the male the endopods of the first and second pair of pleopods are not transformed into a copulatory organ. The basipodite of the first pair of pleopods in the male carries 1-6 spines. The endopod of the maxillula (first maxilla) with two segments; that of the maxilla (second maxilla) with three segments. The outer plates of the uropods with a transverse suture. Photophores absent. Eyes imperfectly developed. All 8 thoracic limbs fully developed.

With one genus and one species, *Bentheuphausia amblyops* (G. O. Sars). Bathypelagic-cosmopolitan. For literature see Einarsson (1942), and Banner (1950).

FAMILY EUPHAUSIIDAE H. & T., 1905.

In the male the endopods of the first and second pairs of pleopods are transformed into a copulatory organ. The basipodites of the first pair of pleopods in the male carry no spines. The endopods of the maxillula and maxilla with one segment. The outer plates of the uropods with no transverse suture. Photophores present, eyes well developed. The eighth, or the seventh and the eighth pairs, of thoracic limbs rudimentary. The second and third thoracic limbs sometimes transformed as prehensile organs.

With 10 genera: *Thysanopoda, Meganyctiphanes, Nyctiphanes, Pseudeuphausia, Euphausia; Thysanoessa, Tessarabrachion, Nematoscelis, Nematobrachion,* and *Stylocheiron.*

Fossil genera (see Peach 1908, p. 61-82): The fossil genus *Anthracophausia* Peach 1908, whose species *A. dunsiana* Peach 1908, and *A. traquairi* Peach 1882 have been regarded as possibly related to *Bentheuphausia,* this is plausible; but, perhaps, they could be compared with *Thysanopoda,* to the late larval and post-larval stages of which they bear a greater resemblance, particularly in the form of the carapace and rostrum, and of the telson. Similarly the fossil species *Crangopsis rhodesi* Peach 1908, *Crangopsis robusta* Peach 1908, and, to a lesser degree, *Crangopsis couttsi* Peach 1908, suggest comparison with *Nyctiphanes* particularly in the antennae, ovisacs, and first and second pleopods. Both sets of species are from the Carboniferous of Scotland.

The remaining species of *Crangopsis,* group 2, of Peach (1908) are strongly suggestive of the Euphausiacea, but those of *Crangopsis,* group 1, with the epimera of the second abdominal segment large and rounded, overlapping the epimera of the first and third segments as strongly suggest the Caridea. The point is of some palaeontological importance, as if the relationship were correct, it would suggest that the Caridea were already an emerging group coterminous with the Euphausiacea in the Carboniferous. The material should be re-examined in the light of modern carcinological knowledge.

I am indebted to Mr. O. Singleton of the Department of Geology, University of Western Australia, for bringing this paper to my notice.

2. THE GENERA AND SPECIES OF THE EUPHAUSIIDAE.

(A) A SORTING KEY TO THE GENERA.

The genera of the Euphausiidae are separable, taxonomically, on a combination of characters. The following working key is provided only for the purpose of the initial generic sorting and recognition of adolescent and adult specimens. It is based on characters afforded by the eyes, the second, third, sixth and seventh thoracic limbs (the eighth thoracic limb is rudimentary in all genera), the presence or absence of ovisacs, and by the nature of the anterior margin of the carapace in the case of *Euphausia* and *Pseudeuphausia.* The genus *Thysanoessa* presents some difficulty when such a restricted set of characters is used as its species vary with respect to the nature of the eyes and the second thoracic limb. With this proviso the genera may be separated into two sections (for sorting purposes only) as follows:

Section 1. None of the thoracic limbs is unusually lengthened or modified as prehensile organs. Cornea of the eye in the adult not separated by a constriction into two hemispheres. With the following genera: *Thysanopoda, Meganyctiphanes, Nyctiphanes, Pseudeuphausia, Euphausia,* and *Thysanoessa* (in part).

Section 2. The second thoracic limb, or the third, or the second and third are lengthened and modified as prehensile organs. The cornea is separated by a constriction into two unequal hemispheres. With the following genera *Nematoscelis, Nematobrachion, Stylocheiron, Tessarabrachion,* and *Thysanoessa* (in part).

Earlier authors, notably Holt and Tattersall, divided the family into two sub-families, the Euphausiinae and the Nematoscelinae, based on the above separation. Since the genus *Thysanoessa* not only contains some species which can be placed in the second, but possesses, also, two species *(T. inermis* and *T. gregaria)* each composed of two series referable to the two sections, the separation is not valid. In spite of this the grouping is a valuable aid to the identification of genera since *Thysanoessa* may be isolated satisfactorily within each section.

The genera of *Section one* may be divided as follows:

A. The endopod of the seventh thoracic limb is developed and segmented.

B. The endopod of the seventh thoracic limb is relatively small but with the usual number (five) free segments, ovisac absent in the female. *Thysanopoda.*

BB. The endopod of the seventh thoracic limb is of the same order of size as those of the other thoracic limbs but consists of two long segments only.

C. The sixth and seventh thoracic limbs possess well developed exopods on both sexes, ovisac absent in the female. *Meganyctiphanes.*

CC. The sixth and seventh thoracic limbs possess no exopods in the female. An ovisac is present in ovigerous females. *Nyctiphanes.*

AA. The endopod of the seventh thoracic limb is rudimentary and non-segmented.

D. The exopods of the seventh thoracic limbs are well developed. There is no ovisac in the female. *Thysanoessa* (in part).

DD. The exopods of the seventh thoracic limbs are rudimentary.

E. The carapace is produced into a truncate frontal plate (cf. Sars 1885, Pl. XV). There is no rostrum. An ovisac is present in ovigerous females. *Pseudeuphausia.*

EE. The carapace is not produced into a frontal plate. A rostrum is present. No ovisac is present. *Euphausia.*

The genera of *Section two* may be identified as follows:

A. The endopod of the second thoracic limb only is lengthened and modified as a prehensile organ.

B. The ultimate and penultimate segments of the endopod of the second thoracic limb are surrounded with stiff bristles. There is no ovisac in the female. *Thysanoessa,* in part.

BB. The ultimate (and in some species, the penultimate) segments of the endopod of the second thoracic limb bear setae which form a bunch of stiletto-like apical bristles. An ovisac is present in the ovigerous females. *Nematoscelis.*

AA. The endopods of the second and third thoracic limbs are lengthened. (Their form is as in *Thysanoessa*). Ovisac not known. *Tessarabrachion.*

AAA. The endopod of the third thoracic limb only is lengthened and modified.

C. The endopod of the seventh thoracic limb is of five segments. Ovisac not known. *Nematobrachion.*

CC. The endopod of the seventh thoracic limb with two segments. Ovisac is present in ovigerous female. *Stylocheiron.*

(B) GENERIC DIAGNOSES AND WORKING KEYS TO THE SPECIES.

(i) The Genus THYSANOPODA Milne-Edwards 1830.

Euphausiidae with the seventh (penultimate) pair of thoracic pair of limbs distinctly developed and of the same structure as the preceding; last pair with the endopod obsolete; but with the exopod well developed. All the true gills provided with an interiorly bent branch, the two posterior pairs rather complex in structure, last pair much the larger and richly arborescent. Flagella of both pairs of antennae greatly elongate. Exognath of second pair of maxillae very small. Photophores as in *Euphausia.* Genotype *Thysanopoda tricuspidata* Milne-Edwards.

Oceanic, mesoplankton. With 13 species (see below).

For literature see Sheard 1942 (the species *Thysanoessa armata* Marukawa 1928 = *Thy. longipes* Brandt; and *Thy. mansui* Marukawa have been included in the genus *Thysanopoda* in error in Sheard 1942), Einarsson 1945, and Banner 1950. *Thysanopoda spinula* Macdonald 1929 is omitted from this conspectus as indeterminable.

The genus has been divided by Hansen (1912, 206) into two well-marked groups.

Group A. Carapace without any distinct cervical groove. Maxillula with the pseudexopod moderately large to very large, at least half its length situated beyond the outer margin of third segment, palp at most moderately long and somewhat over-reaching the third segment. Sixth abdominal segment longer than the fifth.

This group may again be divided.

Section 1. The carapace in the adult with a denticle on or near lower margins near their posterior end.

T. tricuspidata Milne-Edwards 1830; *cristata* Sars 1883; *monocantha* Ortmann 1893; (=? *agassizi* Ortmann); *aequalis* Hansen 1905; *obtusifrons* Sars 1883.

Section 2. Carapace in the adult without denticles on the lower margins near their ends.

T. microphthalma Sars 1885; *pectinata* Ortmann 1893; *orientalis* Hansen 1910; *acutifrons* Holt and Tattersall 1905; *johnstoni* Sheard 1942; *dubia* Banner 1950.

Group B. Carapace with a well-developed cervical groove. Maxillula with the pseudexopod somewhat small, scarcely or not at all over-reaching the outer margin of the third segment, palp very long. Sixth abdominal segment shorter than the fifth.

T. cornuta Illig 1905, and *T. egregia* Hansen 1905.

Keys to the Species of Group A.

In Group A, section 1, separation is difficult. *T. tricuspidata* Milne-Edwards possesses two denticles on or near the lower margin of the carapace, and the male of *T. aequalis* Hansen lacks the spine-shaped process (p^1) on the copulatory organs. The remaining three species can be separated by small differences in the copulatory organs and by differences in the frontal plate, antennular lappet and the dorsal armature of the abdomen. The species are good. Careful reference must be made to the appropriate descriptions and figures.

The species of Group A, Section 2, may be separated as follows (adult males and females):

A. Antennular lappet multidigitate. *T. pectinata* Ortmann 1893.
AA. Antennular lappet not multidigitate.
B. Abdominal segments 4 and 5 slightly acuminate mesially on postero-dorsal margin.
C. Antennal scale reaching to end of second segment. *T. microphthalma* Sars 1885.
CC. Antennal scale reaching beyond the end of the second segment. *T. orientalis* Hansen 1910.
BB. Abdominal segments 4 and 5 smooth on the postero-dorsal margin.
D. Abdominal side plates 1-2-3-4 slightly indented on the lower margin. *T. acutifrons* H. and T. 1905.
DD. Abdominal side plate 1 not indented, 2-3-4 deeply indented on lower margin. *T. johnstoni* Sheard 1942.
DDD. Abdominal side plate 1 not indented, 2-3-4 slightly indented on lower margin. *T. dubia* Banner 1950.

Adult males. Copulatory organs:

A. Spine-shaped process absent. *T. johnstoni* Sheard 1942.
AA. Spine-shaped process (p^1) present.
B. Terminal process (p^2) saw-toothed behind the terminal margin. *T. microphthalma* Sars 1885.
BB. Terminal process not toothed.
C. Terminal process longer than the proximal process (p^3). *T. pectinata* Ortmann 1893.
CC. Terminal process shorter than the proximal.
D. Terminal process evenly rounded at distal end. *T. orientalis* Hansen 1910.
DD. Terminal process acutely pointed at distal end. *T. acutifrons* H. T. 1905.
(The adult male of *T. dubia* Banner 1950 is unknown.)

T. aequalis Hansen and *T. johnstoni* Sheard, although in different sections of the genus, are peculiar amongst the species of *Thysanopoda* in lacking the spine-shaped process of the copulatory organs.

THE SPECIES OF GROUP B.

The two species of group B may be separated as follows:

A. Rostral plate slightly up-curved, tip surmounted by a small tubercle. *T. cornuta* Illig 1905.
AA. Rostral plate down-curved, no rostral tubercle present. *T. egregia* Hansen 1905.

Thysanopoda johnstoni Sheard 1942.

Sheard 1942, 62-63, and ?*T. acutifrons,* Einarsson 1945, 109, *nec* H. and T.

B.A.N.Z.A.R.E. Sta. 111 (44° 11′ S., 143° 36′ E.). N 200, 110-0 metres, 17th March, 1931, surface temperature 12·0° C., surface salinity 34·56, 2 ♂ ♂ 39 mm., 1 ♀ 33 mm. "Warreen" Sta. 25/38 (37° 14′5 S., 150° 23′ E.). N 70, 500-250 metres, 14th August, 1938, surface temperature 14·9° C., surface salinity 35·50, temperature at 300 metres 11·5° C., salinity at 300 metres 35·06, three damaged specimens. Investigator Straits, from stomach of Southern Bluefin Tuna (*Thunnus maccoyii* Castelnau), one adult. "Discovery II," station 2718, 34° S., 153° E., October, 1950, 8 ♂, 3 ♀.

This species falls into Hansen's group A, section 2, possessing the characteristic maxillula, the sixth abdominal segment longer than the fifth and having neither a cervical groove, nor a denticle on the lower margin of the carapace.

They eyes are small, rounded and brown in spirit specimens with the produced frontal plate barely protruding beyond them. The antennule has the first segment the longest, furnished with a lappet similar to that of *T. acutifrons* H. and T. but longer, reaching to the middle of the second segment. The third antennular segment terminates in a small setose lappet. The antennal squama, fringed with long setae along its curved inner margin and on its slightly curved distal end reaches to a little more than halfway up the third antennular segment. The spiniform outer process from the sub-basal segment is thin and tapering, as long as the breadth of the squama.

In the maxilla the distal segment is ovate, slightly longer than the preceding. The maxillula resembles that of *T. pectinata* but the pseudexopod is narrower and the palp relatively longer. Both the maxilla and maxillula are heavily setose with plumose setae. The abdominal segments without trace of any denticles dorsally. The side plates of abdominal segments 1 to 5 resemble those of *T. microphthalma,* figured by Holt and Tattersall (1905, pl. ii) as *T. distinguenda.* However, the emargination of the lower border of plates 2, 3 and 4 is much greater than for that species.

The preanal spine is well developed and is simple in both male and female. The endopod and exopod of the uropods are both slightly longer than the telson, which bears four pairs of dorsal denticles.

The copulatory organs are distinctive. The spine-shaped process is absent. The terminal process, about half the length of the proximal, is sickle-shaped at its distal third, but from the bulb of the commencement of the sickle, a flat membrane runs nearly to the tip. At its distal end this membrane bears, on the outer margin, two very small, rounded prolongations. (The spine-shaped process is absent also in the males of "Discovery II" station 2,718.)

The proximal process is somewhat of the form figured for *T. orientalis* by Hansen (1921). The median lobe resembles that of *T. pectinata* figured by Hansen (1912), but the additional process is not hooked, while there are two secondary additional processes. In all the median lobe bears four processes instead of the three normal to the genus.

A subadult female (length 15 mm.) does not possess a lateral denticle on the carapace. The thylecum of the adult female is very like that of *T. orientalis* Hansen as figured by Einarsson (1942, pl. 1), with the exception that the lower margin of the sternal plate is evenly curved.

GENERAL DISTRIBUTION OF THE GENUS.

The species of the genus are apparently mesoplanktonic in the warmer intermediate waters of the central water masses of all oceans. Apart from the well documented records of *T. acutifrons* in the North Atlantic by Einarsson (1945), insufficient evidence exists as to the distribution of the other species. It is noteworthy that in spite of the very extensive plankton work done in antarctic and sub-antarctic waters no records exist of the presence of the genus there.

(ii) The Genus MEGANYCTIPHANES Holt and Tattersall 1905.

The antennular peduncle is little different in the male and female. Its first segment possesses a membraneous leaflet, backwardly directed. The eighth pair of thoracic limbs only is rudimentary. The seventh pair is distinctly developed but the endopod consists of two elongated segments only. The sixth and seventh thoracic limbs possess an exopod in both sexes. Both the terminal and proximal processes of the petasma are developed. The petasma is nearly as in *Thysanopoda*. The thylecum has no sternal plate but the coxal plates are well developed. They are fused together distally, the sperm mass being deposited in the cavity between them. No ovisacs are present.

With one species, *Meganyctiphanes norvegica* (M. Sars).

The full synonomy is given in Einarsson (1945), where the distribution in the North Atlantic is discussed at length.

(iii) The Genus NYCTIPHANES G. O. Sars 1883.

Antennular peduncle cylindric in the female, subcylindric in the male, with the segments stouter than in the female, the third strongly curved on the outer side. The eighth limb is rudimentary, consisting only of a small exopod. The endopods of the seventh pair are well developed but with two segments only. The sixth and seventh pairs in the female lack exopods.

The terminal and proximal processes of the inner lobe are lacking, but a spine-shaped process is well developed; the lobe itself is produced as an oblong, more or less triangular plate, with the outer margin sinuate and partly serrate.

Paired, pyriform ovisacs form in the female. No thylecum is present, but at least in *N. australis* the sternal plate is long, narrow, and pointed. Anteriorly with two small, oval orifices in the median line, one between the sixth pair, and one between the seventh pair of thoracic limbs. Genotype *Nyctiphanes australis* Sars 1883.

With five species, which are neritic, in cooler sub-tropical waters. The adults are primarily detrital feeders, and their greatest concentration appears to be in the trawl zone.

A Synopsis of the Species of the Genus NYCTIPHANES.

Group A: Lobe from the first antennular segment somewhat small, broader than long, triangular, with the acute end situated above the inner margin of the antennule.

With three species: *N. couchii, N. australis,* and *N. capensis,* separable as follows:

Nyctiphanes couchii (Bell). *Female:* Second antennular segment with a rather large, oblong plate anteriorly terminating in a spine, frequently digitate along its upper margin, and situated at the upper inner edge of the segment near its end. *Male:* Second antennular segment with a close row of generally 3 (3-5) spiniform, strong, partly plumose setae on the inner side of the segment near its base. Median lobe of the copulatory organs reaching rather near its base. Median lobe of the copulatory organs reaching near the end of the lateral process. Length generally 14-17 mm.

For literature and synonomy see Einarsson (1945). For distribution see Einarsson (1945). The species is detrital feeding in the adult and is prominent in the trawl zone, i.e. in the detrital bearing, bottom water layers of the neritic zone. Its temperature range is 8° C. to 20° C. in the coastal waters of the North Atlantic, North Sea, and Mediterranean. The temperature range roughly parallels that of *N. australis* in the South Western Pacific coastal waters.

N. australis G. O. S. *Female:* Second antennular segment with the upper inner edge terminating in a minute spine, but without any raised plate. *Male:* Second antennular segment with a low, raised plate project-

ing from the inner upper edge near the distal end; third segment without any spiniform setae, but with some quite minute hairs distributed along the inner side. Median lobe of the copulatory organs reaching fully the end of the lateral process. This species is discussed in detail later in this report.

N. capensis Hansen 1911. *Female:* Second antennular segment with the upper inner margin terminating in a minute or quite rudimentary spine, but without any protruding plate. *Male*: Second antennular segment without any plate at the end of the upper inner edge; third segment with the close row of nearly spiniform setae placed somewhat from the base or at the middle of the inner side of the segment. Median lobe of the copulatory organs reaching scarcely the middle of the lateral process. Length of the largest male 12·3 mm. Off Cape Blaize, southern end of Africa.

Synonomy.

Nyctiphanes capensis Hansen 1911.

N. australis nec Sars, Stebbing 1905 p. 113, 1910 p. 399. *N. capensis* Hansen 1911, p. 19-20. *?N. africana,* Zimmer, 1912, p. 3. *N. capensis,* Hansen, 1912, p. 266. Einarsson, 1945, p. 44.

Group B: Lobe from the first antennular segment large, conspicuously longer than broad, not triangular, with the short, acute tip turned mainly or totally outwards.

With one species, *N. simplex.*

N. simplex Hansen 1911. *Female:* Second antennular segment with the upper inner margin distally raised in an oblique spine or an obliquely triangular, acute tooth. *Male:* Second antennular segment at most with a small, raised, acute protuberance on the usual place; third segment with the row of spiniform setae situated as in *N. couchii.* Median lobe of the copulatory organs abbreviated, having no part along the outer margin of the lateral process, length 11-16 mm.

Distribution: Neritic, East Pacific Lat. 35°. N. to 6° S.

References.

N. simplex Hansen 1911, p. 20; 1912, p. 27, figs.; Esterly, 1914, p. 8-10; Hansen 1915, p. 70-71; Boden, 1951.

(iv) Genus PSEUDEUPHAUSIA Hansen 1910.

As in *Euphausia,* but different in the following characters. Carapace produced into a long frontal plate with the broad end transversely cut off, without rostrum; lateral margin with a small tooth near the posterior end. Endopod of the sixth distal segments scarcely more than half as long as on the fifth pair; in the female that endopod is only half as long as the fifth pair with the third segment a little expanded and the third and fourth together strongly curved forming somewhat less than half a circle for the reception of the ovisac; while the three terminal segments of the fifth pair are only half as long as in the male.

Copulatory organ; inner lobe with 2 small spine-shaped processes, the lateral process of the median lobe replaced by a relatively large, oblong leaf-shaped plate, the auxiliary lobe wanting and the setiferous lobe narrow and without setae.

Ovigerous females carry an oblong-triangular ovisac, rounded anteriorly, and posteriorly divided by a median incision.

Genotype *Pseudeuphausia latifrons* (Sars) Neritic, Trawl-Zone. Tropical and Sub-tropical. Two species. *P. latifrons* (G. O. Sars), *P. colosi* Torelli. The synonomy of *P. latifrons* is given in Tattersall 1936 and 1939. The description of *P. colosi* Torelli 1934 has not been seen by me.

(v) The Genus EUPHAUSIA Dana 1850.

This genus is ill-defined and will doubtless, be divided when the species are better known.

Rostrum and lateral denticles of carapace variable. Eyes undivided. Antennular peduncles not showing sexual dimorphism with the basal segment carrying a lappet in some species, both flagella elongate. Maxilla with terminal segment broad and exopod small. Anterior six pairs of thoracic limbs subsimilar in structure, none elongate. Exopod of seventh and eighth thoracic limbs represented by an unjointed styliform segment. Endopod lacking on both seventh and eighth limbs in both sexes.

Male copulatory organs with the basal portion of the terminal process of the inner lobe broadened into a "foot" of varying protuberance, the "heel" also of varying size. The proximal process well developed. The spine-shaped process and the additional process lacking in almost all species. The lateral process may carry one to three teeth. Genotype *Euphausia superba* Dana 1850. Oceanic, pelagic.

With 34 species, some dubious (see species lists in Tables 1 and 2). The genus has been divided into four groups by Hansen (1911). This division has been followed herein, with some modifications.

For a critical discussion of certain natural groupings see John (1936). Where it has been possible, his findings on the systematic position of the species have been followed in the present taxonomic treatment.

GROUP A.

Species with two pairs of lateral denticles on the carapace. No dorsal process on the third to fifth abdominal segment. The male copulatory organ, with a slender, thin walled secondary process near the distal end of the proximal process. Hansen (1911), and John (1936).

The adults and sub-adults of the species may be separated, on a purely preliminary basis, by characters on the segments of the antennular peduncle. (See key to species.) Detailed reference to descriptions and figures is required beyond this point.

This is a natural group which includes seven species, *E. krohnii, E. eximia, E. americana, E. recurva, E. diomedeae, E. mutica,* and *E. brevis.*

GROUP B.

Species with a single (rarely no) pair of denticles on the lateral margin of the carapace. No dorsal process generally on the third abdominal segment but sometimes a small spinous process *(E. vallentini)* sometimes a dorsally produced, localised heel *(E. similis var armata).*

This is the classic Group B of Hansen. It has been discussed by John (1936), who has concluded that the group contains a natural group. Hansen's grouping consisted of the following species: *E. lucens, E. frigida, E. superba, E. crystallorophias, E. similis, E. tenera* and *E. pacifica.* John suggests, on the basis of characters afforded by the petasma, that a natural group can be isolated consisting of the species *E. crystallorophias, E. superba, E. frigida, E. vallentini* and *E. lucens.* This appears well founded on both the reproductive and distributional characteristics of the species. Accordingly I have added *E. vallentini* from Group C to the present keys to cover those specimens of *E. vallentini* in which the spine on the third abdominal segment is obsolete.

GROUP C.

Species with a single pair of lateral denticles on the carapace. The dorsal surface of the third abdominal segment is produced posteriorly in the mid-line, forming an acute, compressed, spiniform process.

E. vallentini, E. similis var *armata, E. lamelligera, E. distinguenda, E. sibogae, E. mucronata, E. fallax, E. gibba, E. pseudogibba, E. hemigibba* and *E. paragibba.*

E. alvae Boone, and *E. consuelae* Boone (? = *E. fallax* Hansen) included in Group B by Boone belong in Group C. They are somewhat difficult to assess. It would appear that the nomenclature of certain of the processes of the petasma (notably p^2 and p^3) has been reversed both in the description and drawings.

The variety *E. similis* var *armata* Hansen (which should be regarded as a species in its own right) and the species *E. vallentini* Stebbing have been included in the key for purely sorting purposes, although *E. similis* var *armata* must be included, naturally, with *E. similis* in Group B; while *E. vallentini* groups, naturally with the *E. lucens, frigida, superba, crystallorophias* complex, as demonstrated by John (1936).

GROUP D.

Species with a single pair of lateral denticles on the carapace. A well developed dorsal process on the third abdominal segment, and conspicuous dorsal denticles or processes on the fourth and fifth segments.

This is a natural group with 4 species: *E. spinifera, E. longirostris, E. triacantha,* and *E. hanseni.*

THE SPECIES OF GROUP A.

The following working key is modified from the table given by John (1936, p. 241) and is based on the processes of the first and second segments of the antennular peduncle in the adult and adolescent; and secondarily on the copulatory organ of the adult male.

A. Lobe of the first antennular segment pectinate.

B. Second antennular segment, distal end dorsally with no tubercles. *A. americana* Hansen.

BB. Second antennular segment, distal end dorsally with two tubercles.

C. Terminal process (p^2) bearing a slender spiniform process toward the tip; process on the proximal process (p^3) evenly curved. *E. eximia* Hansen.

CC. Terminal process without spine; process on the proximal process trifid. *E. krohnii* (Brandt).

AA. Lobe of the first antennular segment not pectinate.

D. Second antennular segment, distal end dorsally with two tubercles *(E. diomedeae);* or a spine and tubercles *(E. recurva).*

E. Male with reflexed simple leaflet on first antennular segment, this lobe bifid and upstanding in female. *E. recurva* Hansen.

EE. Male and female with the lobe on the first antennular segment bifid and forwardly pointing. *E. diomedeae* Ortmann.

DD. Second antennular segment with a forwardly directing spine on the outer distal angle. No tubercle on the inner distal angle. *E. brevis* Hansen.

DDD. Second antennular segment with neither spines nor tubercles on the distal end. *E. mutica* Hansen.

Since the species are referred to in somewhat scattered literature, references are given to papers containing the chief references and synonomy and discussion of each species. The lists do not represent a complete reference but these can be obtained from the papers cited below.

E. americana Hansen (1911); Tattersall (1924), 17; John (1936), 240-241.
Distribution: North and South Atlantic central waters.

E. eximia Hansen (1911); Hansen (1915), 75-76; John (1936), 240-241.
Distribution: Western North Pacific central water.

E. krohnii (Brandt) 1851; Hansen (1915), 71-74; John (1936), 240-241; Einarsson (1945), 128.
Distribution: Central water mass of North Atlantic central water, thence to the Mediterranean. Northern limit of spawning area 10° C. (Einarsson, 1945).

E. recurva Hansen (1905); Esterley (1914); Hansen (1915); Tattersall (1924); John (1936).
The wide distribution of this species is discussed in some detail in the body of this paper.

E. diomedeae Ortmann (1894); Hansen (1910), (1915); John (1936); Tattersall (1939).
Distribution: Pacific and Indian Ocean Equatorial water; Red Sea.

E. brevis Hansen (1905); Tattersall (1939); John (1936).
Distribution: Equatorial waters of all oceans; Mediterranean, widespread and common.

E. mutica Hansen (1905); *restricted,* Hansen (1910), (1915).
Distribution: Equatorial waters of all oceans.

SPECIES OF GROUP B.

A. Hind margin of first and second abdominal segment straight dorsally.

B. Distal segment of the mandibular palp, long and slender. *E. superba* Dana 1852.

BB. Distal segment of the mandibular palp, short and broad.

C. Antennular lobe developed in both male and female.

D. Antennular lobe well developed in forming an anteriorly broadly rounded plate. (The rostrum a short, sharp triangle.) *Euphausia vallentini* Stebbing 1900 (also see Group C).

DD. Antennular lobe small and triangular.

E. Antennular lobe small but conspicuous about as broad as long and protruding forwards and upwards. The rostral plate as a rule is a distinct low triangle, broader than long to nearly rudimentary. *E. lucens* Hansen 1905.

EE. Antennular lobe a very small, triangular lobe, distinctly broader than it is long, the dorsal keel of the third antennular segment in side view, lower than in *E. lucens,* with the upper margin straight and the distal angle nearly rectangular. Rostral plate as in *E. lucens. E. frigida* Hansen 1911.

EEE. Antennal lobe produced into a triangulate, dentate process (set obliquely) that projects over the second segment. Rostral plate barely produced. *E. pacifica* Hansen 1911.

CC. Antennular lobe not present in male or female *(E. crystallorophias)*; not present in male, present as a very small triangular process in female. *(E. tenera.)* Frontal plate produced to an acute rostrum.

G. Eyes, with the cornea wider than the corneal cup. *E. crystallorophias* Holt and Tattersall (1905).

GG. Eyes, with the cornea narrower than the corneal cup. *E. tenera* Hansen 1905.

AA. Hind dorsal margin of the first and second abdominal segments dorsally with a produced rounded part. Rostrum long and acute antennular lobe directed upwards and forwards, bifid, the inner lappet longer than the outer. *E. similis* Sars 1885.

References to papers containing descriptions and synonomy of these species of this important group are as follows:

E. superba Dana 1852; Tattersall, 1908; John, 1936; Fraser, 1936; Bargmann, 1937, 1945.
Distribution: Antarctic.

E. vallentini, Stebbing 1900; Tattersall, 1908; Hansen, 1913; John, 1936.
Distribution: Sub-antarctic with the exception of the warmer water.

E. lucens Hansen 1905; Hansen, 1911; John, 1936.
Distribution: Warm water of the sub-antarctic zone, cool water of the sub-tropical zone.

E. frigida Hansen 1911; Hansen, 1911; John, 1936.
Distribution. Antarctic.

E. pacifica Hansen 1911; Hansen, 1912, 1913, 1915; Banner, 1950.
Distribution: North Pacific, 25° N. to 59° N.

E. crystallorophias Holt and Tattersall 1905; Tattersall, 1908; John, 1936.
Distribution: Neritic antarctic.

E. tenera Hansen 1905; = (*E. gracilis* Sars 1885, *nec* Dana 1852); Hansen 1910, 1913, 1915, 1916.
Distribution: Tropical and warm sub-tropical areas.

E. similis Sars 1885; Hansen, 1911; Zimmer, 1914; John, 1936.
Distribution: Cool sub-tropical and warm sub-antarctic.

THE SPECIES OF GROUP C.

Most of the species in this difficult section occur in tropical and warm sub-tropical oceans (see fig. 2). The species are small, many of the diagnostic characters are ill-defined, and the following separating key must be used with discretion. Detailed reference to the respective descriptions is essential. The *habitus* of the various species is sufficiently different to separate them quite reasonably in the sorting dish. As an example, *E. pseudogibba* may be separated from the more slender, graceful species, *E. paragibba* and *E. hemigibba,* by its relatively clumsy appearance; but no distinctive characters can be isolated which correspond with this difference. Again, specimens may be grouped in terms of resemblances and differences existing in the sculpturing of the dorsal surface of the antennular peduncle segments (including that of the third segment), and the males of each of the groups so sorted correspond consistently in their petasma characters with known species groupings. From this and from the known distributional characteristics and from differences in the petasma it would appear that most of the species are taxonomically "good" but the section is in need of thorough revision. *E. vallentini* and *E. similis* var. *armata* do not belong naturally in this group; but the species are retained in the working key, below, as the abdominal spines which they possess are superficially like those of the *"gibba"* group.

A. Projection from the dorsal midline of the third abdominal segment varying from a rounded prominence to a short based, truncate keel to a short based spinous keel.

B. The lobe of antennular segment one, strong, bidentate, projecting over the second segment. Rostrum strongly projecting. *E. similis* var. *armata* Hansen = (*E. similis* var. *lobata* Zimmer 1914) ?= (*E. similis* var. *crassirostris* Hansen 1910).

References, see John 1936.

BB. The lobe of antennular segment one, strong and forming an anteriorly broadly rounded plate. Rostrum a short, sharp triangle. *E. vallentini* Stebbing 1900 (see also key to group B).

AA. Projection from the dorsal midline of the third abdominal segment a spinate extension of the region of the dorsal midline of the margin of the segment.

C. Fourth abdominal segment similarly produced dorsally (but into a smaller process).

D. Antennular segment one, lobe deeply bifid. (Rostrum short, not produced. Lobe absent on the second antennular segment.)

E. mucronata Sars 1885.

Distribution: Peruvian current. Description: Hansen, 1912.

DD. Antennular segment one, lobe a triangulate, acuminate process. (Rostrum short, produced. Lobe absent, on the second antennular segment.)

E. alvae Boone 1935.

Distribution: Flores Strait.

CC. Fourth abdominal segment not produced dorsally.

E. Antennular segment one, lobe absent. (Lobe also absent on the second antennular segment. Rostrum acute, very short.)

E. sibogae Hansen 1910.

Distribution: East Indian Archipelago.

EE. Antennular segment one. Lobe present, rudimentary.

F. Antennular segment one, lobe rudimentary, plate-like, shallowly incised in centre. Rostrum very small, acute; second antennular segment with a small ear-like lobe.

E. distinguenda Hansen 1911.

Distribution: Tropical Pacific and Indian Oceans. Description: Hansen 1911, 1912.

FF. Antennular segment one; lobe well defined.

G. Antennular segment one; lobe projecting, roundly cleft at forward end. (The second antennular segment ends in a large rounded lamella covering half of the third segment; no rostrum.)

E. lamelligera Hansen 1911.

Description: Hansen 1912; References Tattersall 1939.
Distribution: Tropical Pacific, Indian Ocean.

GG. Antennular segment one; lobe projecting, pointed.

H. Lobe of the second antennular segment, absent. (The spine of the third abdominal segment compressed and short, acute, at its base a carinated plate; rostrum, short, very acute.)
E. gibba G.O. Sars 1885.

Description Hansen 1911, 1912. Distribution: Warm sub-tropical South Pacific.

HH. Lobe of the second antennular segment, present.

I. Lobe of the second antennular segment projecting, sub-rectangular, short and broad. (Rostrum small, but produced, pointed.)

1. *E. gibboides* Ortmann 1893. ?= (*E. sansoi* Torelli 1934).

Description: Hansen 1912; references Tattersall 1939.
Distribution: All tropical oceans.

2. *E. fallax* Hansen 1916. ?= (*E. consuelae* Boone 1935). (The separate identity of this species has been retained in Tables 1 and 2.)

Distribution: Philippines; West Pacific.

E. gibboides and *E. fallax* can be separated only by small characters of the petasma.

II. Lobe of the second antennular segment represented only by a small, sharp tooth.

1. *E. Pseudogibba* Ortmann 1893.

Descriptions: Hansen 1910, 1911, 1912. Distribution: Tropical oceans.

2. *E. paragibba* Hansen 1910.

Description: Hansen 1912; Illig 1930. Distribution: Tropical Indian and Pacific.

3. *E. hemigibba* Hansen 1910.

Description: Hansen 1915. Distribution: Sub-tropical Atlantic and sub-tropical Indian.

A discussion of the above three species as a natural group (separable mainly by differences in the petasma) is contained in John (1936) where the structure of the petasma is discussed. On that basis it would appear that the species *E. gibboides* Ortmann and *E. fallax* Hansen could also be added to the natural group. If this were so the species *E. gibba* Sars, *E. distinguenda* Hansen, *E. lamelligera* Hansen and *E. sibogae* could be regarded also as comprising a second natural group based on the common petasma characters.

THE SPECIES OF GROUP D.

A. Hepatic spine on the carapace.

B. Antennular leaflet multidigitate. *E. spinifera* G. O. Sars 1885.

BB. Antennular leaflet bifid. *E. hanseni* Zimmer.

AA. No hepatic spine on the carapace.

C. Posterior margin of the third to the fifth abdominal somites incised. Lateral denticles of the carapace situated above the margin. Antennular leaflet bifid. *E. longirostris* Hansen.

CC. Posterior margin of the third to fifth abdominal somites entire. Lateral denticles of the carapace, marginal. Antennular leaflet bifid. *E. triacantha,* Holt and Tattersall.

The synonomy of the species is given in Tattersall (1925). A tabular key to the first and second antennular segments (together with figures of the copulatory organs of this group) is given by John (1936), who also discusses its natural relationships and distribution and presents some details of the life history of *E. spinifera*, *E. longirostris* and *E. triacantha.*

The principal ranges of the species are as follows:

E. triacantha: Circumpolar in the sub-antarctic zone, thence southwards into the antarctic zone.

E. longirostris: Circumpolar in the warmer sub-antarctic zone waters.

E. spinifera: Circumpolar in cooler sub-tropical waters, principally in areas of formation of central water masses. In the Tasman Sea at least to Lat. 38° S.

E. hanseni: In eastern South Atlantic central water, in the Benguela current, and perhaps, in the Guinea current.

(vi) The Genus THYSANOESSA Brandt 1851; (Hansen, 1911).

Rostrum always good-sized, rather long to very long. Eyes sometimes almost completely circular, generally distinctly or considerably higher than broad, narrowing upwards and most frequently above the middle divided by a transverse constriction. Antennulae with the peduncles showing sexual differences and with their two distal segments slender in the female; upper flagellum at most somewhat longer than the peduncles, frequently much shorter. The six anterior pairs of thoracic limbs with full number of segments; second pair frequently elongate and thickened, and with setae or spines along the whole margin of sixth and seventh segments; seventh pair with the exopod normally developed, the endopod wanting in the males, in adult females, always present, articulated to the broad, exopod-bearing segment, with one or two segments, and from more than half as long as to somewhat longer than the exopod; eighth pair without endopod, while the exopod is somewhat styliform, naked or with setae at the end. Copulatory organs with the spine-shaped process thin and curved as in *Thysanopoda,* the two other processes of the inner lobe, and the lateral process well developed but the additional process is either lacking or poorly developed. The other characters as in *Nematoscelis.* A thylecum is present in the female but there are no ovisacs. Genotype *Thysanoessa longipes* Brandt 1851. With nine species.

Working Key to the Species of the Genus THYSANOESSA Brandt.

A. Third, fourth, and fifth abdominal segment with a compressed dorsal keel.

B. Third abdominal segment generally with a good-sized process from the end of its strong dorsal keel, and small dorsal processes or denticles on the three following segments. Eyes considerably higher than broad, with transverse constriction. Lateral margins of the carapace with a denticle at the middle. Second pair of limbs elongate and robust. *T. longipes* Brandt 1851.

Distribution: North Pacific–Sub-arctic. For synonomy, see Banner (1950).

BB. Third abdominal segment without any process from its strong dorsal keel, but a good-sized process on the fourth segment and distinctly smaller processes on the two following segments. Eyes a little higher than broad, without constriction. Lateral margins of the carapace without denticles. Second pair of limbs slightly, or at most a little longer, and somewhat stronger than the third. *T. spinifera* Holmes 1900.

Distribution: Sub-arctic to cool sub-tropical waters of the North Pacific. For synonomy see Banner (1950).

AA. Third, fourth and fifth abdominal segments without dorsal keels.

C. Lateral margins of the carapace without any denticle.

D. Sixth abdominal segment much shorter than the sum of the two preceding segments, with a strong spine from its upper distal end. Rather large and somewhat robust species. (Second limb either elongate, *neglecta* series; or normal, *inermis* series.) *T. inermis* (Kroyer) 1846.

Distribution: Sub-arctic and cool sub-tropical North Atlantic and North Pacific waters. For detailed references see Einarsson (1945), and Banner (1950).

DD. Sixth abdominal segment elongate, almost or fully as long as the sum of the two preceding segments, with a strong spine from its upper distal end. Rather large and somewhat robust species. Second thoracic limb always elongate. *T. longicaudata* (Kroyer) 1846.

Distribution: Sub-arctic and cool sub-tropical North Atlantic waters. For detailed discussion and references see Einarsson (1945).

CC. Lateral margins of the carapace with a denticle. (No spine from the upper end of sixth abdominal segment.)

E. Denticle before the middle of the lateral margin of the carapace. Eyes nearly circular, without constriction. Second pair of limbs not elongate, shaped as the third. *T. raschii* (M. Sars), 1864.

Distribution: Sub-arctic to arctic; North Atlantic, North Pacific. For synonomy and detailed discussion see Einarsson (1945).

EE. Denticle conspicuously behind the middle of the lateral margin. Eyes conspicuously higher than broad, with constriction. Second pair of limbs elongate, differing from the third.

F. Sixth abdominal segment somewhat and generally considerably shorter than the sum of the two preceding segments.

G. Setae along the lower margin of fifth and sixth segment of second to fourth pairs of limbs thin, not ciliated, much shorter than some of the terminal setae of seventh segment. Terminal process of the copulatory organs not widened towards the truncate end; proximal process with about the same breadth from the middle to the obliquely truncate end, and the terminal very short part bent somewhat outwards, obliquely truncate with the inner front angle produced into a tooth. *T. parva* Hansen 1905.

Distribution: Warm waters of the eastern and north-western Atlantic. Synonomy in Hansen (1915).

GG. Setae along the lower margin of fifth and sixth segment of third to fifth pairs of legs strong, conspicuously ciliated as long as, or longer than, the terminal setae of seventh segment. Terminal process of the copulatory organs somewhat expanded towards the terminal margin, which is feebly convex and finely serrate along the front side, while the inner distal angle is obtuse but scarcely rounded, the outer acute and produced; proximal process with a large, triangular, wing-like expansion serrate along the distal margin and occupying the major part of the distal half of the outer margin, while the part beyond this expansion is short, slender, somewhat curved, sub-acute and with teeth on the outer margin.

T. gregaria G. O. Sars 1885.

Distribution: Sub-tropical in the Southern and probably Northern Hemispheres. This species is discussed further, later in this report.

FF. Sixth abdominal segment almost or fully as long as the sum of the two preceding segments.

H. Antennulae with the upper flagellum somewhat or considerably longer than the sum of the two distal peduncular joints. Terminal process of the copulatory organs a little expanded on the inner side towards the terminal margin which is convex with fine saw-teeth along the front side; proximal process with the end somewhat expanded and curved backwards, with the terminal margin transverse and serrate. (Seen from the side this terminal part is quite thin and somewhat curved.)

T. vicina Hansen 1913.

Synonomy in Tattersall (1924). Distribution: Sub-antarctic to the sub-tropical convergence.

HH. Antennular with the upper flagellum somewhat shorter than the sum of the two distal peduncular joints. Terminal process of the copulatory organs distally expanded at both sides and especially outwards, with the terminal margin long, oblique, conspicuously emarginate, without serration, while the terminal inner part is a projecting, broadly rounded lobe, the terminal outer part subtriangular with the free angle narrowly rounded; proximal process with a very short terminal part strongly curved, slender at the base of the curvature and the end itself distinctly broader with the margin transverse.

T. macrura G. O. Sars 1885.

Synonomy in Tattersall (1924), and see Rustad (1930).

Distribution: Antarctic and sub-antarctic in cooler waters than *T. vicina* Hansen.

(vii) The Genus TESSARABRACHION H. J. Hansen 1911.

Carapace with the frontal plate small, triangular, short and much broader than long; a rostral process is wanting. Eyes very large, higher than broad, distinctly constricted not much above the middle. Antennulae as in *Thysanoessa:* The first segment without distal lobe and very much broader than the two other peduncle segments, which are slender in the female, while in the male the third segment especially is thicker; the upper flagellum depressed and shorter than the lower which is compressed; both flagella broader in the male than in the female. Antennulae as in *Thysanoessa;* the peduncle of the endopod elongate with its proximal segment more than twice as long as the distal.

Maxillulae with the pseudexopod and the palp moderately large. Maxilla very broad, both laciniae with the inner margin incised; fourth joint short and somewhat small, exopod produced along the outer margin of fourth joint terminating beyond its end. Endopod of the maxillipeds (first thoracic limbs) with the fourth segment extremely elongate, almost four times as long as the sum of the three distal segments, fifth and sixth segments being very short.

Thoracic limbs about as in *Thysanoessa* excepting that both second and third pairs are very elongate, subsimilar; the structure of these limbs is in the main like the second pair in a species of *Thysanoessa* where this pair is very elongate. The three following pairs with the full number of segments in the endopods; sixth pair with the exopod normally developed, while the endopod is in the female with the two segments, very slender, and slightly longer than the exopod, but wanting in the male. Eighth pair in both sexes without endopod, while the somewhat small exopod is one-segmented, styliform. Abdomen as in *Thysanoessa.* All luminous organs are present. Copulatory organs of first pleopods reduced. The setiferous lobe and the auxiliary lobe with its hooks are well developed, while a median lobe is not marked off from the inner lobe, which has no processes, but only two or three fine marginal spines.

The genus differs from *Thysanoessa* in having no rostral process, while the second and third pairs of thoracic limbs are very elongate and sub-similar; furthermore, the structure of the maxillipeds (first thoracic limb) differs much from that in *Thysanoessa* and all other genera.

With one species *Tessarabrachion oculatum* Hansen 1911.

Distribution: Northern North Pacific. For references see Banner (1950).

(viii) The Genus NEMATOSCELIS G. O. Sars 1883.

Rostrum variable. Eyes with transverse constriction. Antennular peduncles slender and elongate in the female, shorter and thicker in the males. Mandibular palps small. Second thoracic limbs elongate with setae only on the distal end of the propodus and dactylus. Seventh thoracic limbs with the endopod composed of two segments in the female, wanting in the male; exopod present in both sexes. Eighth thoracic limbs represented by a simple, setose plate.

The copulatory organs possess the three processes on the inner lobe, but the spine-shaped process is nearly straight and nearly parallel with the two other processes which are inserted on the end of the lobe. The lateral process is never hook-shaped and the additional process is wanting. Genotype *Nematoscelis megalops* Sars. With 7 species.

The genus inhabits slope and ocean waters in sub-tropical and tropical waters of both Hemispheres. The taxonomy of the species is not well known and knowledge of their distribution is likewise slender.

The Species of the Genus NEMATOSCELIS Sars.

The species may be divided into two groups following Hansen (1910, 1911, 1912, and 1916).

GROUP A.

Maxillulae with a pseudexopod well developed. Second (the elongate) pair of limbs with long spines both from the terminal segment and from the distal angle of the penultimate segment. Third to sixth pair of limbs with the full number of segments, therefore three segments beyond the knee.

The two species, *N. megalops* and *N. difficilis,* are separable on petasma characteristics only.

A. Inner lobe of the copulatory organs with the spine-shaped process slender about one third the length of the terminal process, and with the proximal process much shorter and more slender than the terminal process. *N. megalops* G. O. Sars 1883 (and 1885).

Distribution: Sub-tropical North Atlantic and South Atlantic. References Einarsson (1945) and see discussion on thylecum, Einarsson (1942).

AA. Inner lobe of the copulatory organs with the spine-shaped process stout and about one half the length of the terminal process, and with the proximal process only moderately shorter, and as stout as the terminal process. *N. difficilis* Hansen 1911.

Distribution: Sub-tropical in the north and south Pacific. The distribution is discussed later in this report. For references see Banner (1950).

The above two species are considered by some authors, notably Einarsson (1942) on the basis of the identity of the thylecum, to be the same. Pending further comparison it would be better to regard them as separate in order that distribution may be clearly recorded.

GROUP B.

Maxillulae without pseudexopod. Second pair of limbs with long spines only from the terminal segment. Third and fourth pairs of limbs with but two segments beyond the knee, fifth and sixth pairs with one segment beyond the knee.

This section of the genus contains five species narrowly separating by differences in the copulatory organs. These are *N. microps* Sars 1883, *N. atlantica* Hansen 1910, *N. gracilis* Hansen 1910, *N. tenella* Sars, and *N. lobata* Hansen 1916.

Einarsson (1942), on the basis of the thylecum, distinguishes between *N. microps, N. atlantica and N. gracilis.* I can offer no guidance in this separation as I have not seen representative material of *N. atlantica* or *N. gracilis.*

Specimens generally referable to *N. microps* Sars have been obtained from the northern range of "Warreen" traverses but in these cases the copulatory organ tends more to that of *N. lobata* while the thylecum is somewhat intermediate between that figured for *N. microps* Sars and *N. atlantica* Hansen, by Einarsson (1942).

(ix) The Genus NEMATOBRACHION Calman 1905.

Carapace with a cervical groove, usually without denticles on the lateral margin. Eyes with a transverse constriction. Antennular peduncle not showing sexual dimorphism; flagella long and slender. Mandible with a three segmented palp. Maxillules with or without pseudexopod. Maxillae relatively broad. First and second thoracic limbs of similar size, the second with the dactylus short and broad. Third limb elongate, the segments without setae or spines except for the dactylus which bears six stiff spines, merus with a sharp bend near the proximal end; carpus and propodus elongate and thin. The following limbs small and decreasing in size anteriorly. Endopod of eighth limbs absent, exopodite normal. Copulatory organs with all lobes present and with all processes, including the additional process, present and well developed.

Genotype *Nematobrachion boopis* (Calman).

Distribution: Sub-tropical and tropical oceans.

With three species which may be separated in the following key, modified from Hansen (1912).

The Species of the Genus NEMATOBRACHION Calman 1905.

A. Frontal plate obtuse without rostral process. Eyes dark brownish; upper section more than twice as deep as the lower. Antennular peduncles without any process from the distal outer angle of first segment and with an at most slightly produced, acute angle above near the distal outer corner of second segment. No dorsal denticles or processes on the abdominal segment.

N. boopis (Calman) 1896.

Distribution: Tropical and sub-tropical oceans. For synonomy and discussion see Tattersall (1924); and Ruud (1936).

AA. Frontal plate terminating in a slender rostrum. Eyes black, with the upper section only somewhat deeper than the lower. Antennular peduncles with a long spiniform process from the distal outer angle of second segment. Conspicuous dorsal denticles on at least two abdominal segments.

B. The process from second antennular segment with, at most the proximal half plate-shaped, and the distal half or the major part spiniform. Third to sixth abdominal segment each with a single dorsal spiniform process from the hind margin.

N. flexipes (Ortmann) 1893.

Tattersall (1924) and Banner (1950) record the presence of denticles on the carapace margin; Tattersall, in immature specimens only; Banner, without that reservation. "Warreen" specimens possess denticles in all but the largest specimens, i.e. they were absent in fully mature individuals.

Distribution: Tropical oceans.

BB. The process from second antennular joint is a large, oblong plate slightly acuminate at the acute end. Fourth and fifth abdominal segments each with a dorsal row of three sharp denticles from the hind margin, but no denticles from the other segments.

N. sexspinosus Hansen 1911.

This species apparently from deep tropical and sub-tropical waters, is very rare and little known. For reference see Hansen (1912), and for additional characters see Tattersall (1926).

(x) The Genus STYLOCHEIRON G. O. Sars 1883.

Form of body and rostrum variable; carapace without lateral denticles. Eyes usually divided. Antennular flagella of a small number of elongate segments with the second and third segments elongate and thin in the female, shorter and thicker in the male, and with the distal segments round in the female, flattened and sometimes expanded in the males. Antennal peduncle extending beyond the end of the squame. Mandibles without palps. Maxillules without pseudexopod. Maxillae with endopod reduced and the endite of the protopodite without the incision separating them into two lobes. Second thoracic limbs similar to first thoracic limbs. Third limbs elongate, with the merus and carpus elongate and without setae. The propodus of the third limb is swollen and bears stiff setae, that meets those of the short dactylus in opposition forming a grasping organ which in some species approaches a true chela. The limbs following are short and decrease in size posteriorly; the endopod of the sixth is composed of three segments in the females and of three or less in the males; that of the seventh is composed of two segments in the female, and is rudimentary in the male. The eighth endopod is lacking in both sexes. There are three photophores only.

First pleopods of the adult male with the inner lobe coalescing with the median lobe for almost its entire length and bearing the usual three processes. Median lobe bearing the lateral process near the point of union with the lateral lobe. Additional process not present. All processes quite simple. Ovisacs present in the female.

Genotype *Stylocheiron carinatum* G. O. Sars.

Oceanic, the majority of the species tropical and sub-tropical.

With 10 species, one of which is doubtful, divided into three taxonomic groups on the armature of the propodus and dactylus of the elongate pair of limbs.

The Species of the Genus STYLOCHEIRON Sars.

GROUP A.

Species with the lateral setae only on the penultimate segment of the elongate pair of limbs. A small spur on the inferior margin of the antepenultimate segment at the forward end. (See Sars 1885, pl. 26.) *Stylocheiron carinatum* Sars 1885.

The copulatory organs are described in Hansen (1910); for refences see Tattersall 1924. Distribution: Tropical and sub-tropical oceans.

A closely related species, *S. armatum*, has been described by Colosi (1917), from the Indian Ocean and Caribbean Sea, based on small differences in the petasma and in the elongate limb. (In view of the variations in the petasma of *S. maximum* Hansen found by Banner (1950) the species must be treated with reserve.)

GROUP B.

Species with the elongate limb terminating in false chelae, having no real immovable finger, but a very long and strong curved spine from the last segment (near this spine several others) opposed by one or two long, curved spines arising laterally on the penultimate segment. There is no spur on the antepenultimate segment. See figures in Sars (1885); Hansen (1910); and Banner (1950).

With five species, *S. longicorne* G. O. Sars 1885, *S. suhmii* Sars 1885, *S. elongatum* Sars 1885, *S. insulare* Hansen 1910, *S. affine* Hansen 1910. Redescriptions are contained in Hansen (1910), and (1912). A recent synonomy of *S. longicorne* Sars is contained in Banner (1950). The species are separated by small differences in the eyes, the antennal squama, the shape of the sixth abdominal segments and by small differences in the copulatory organs. The differences in these characters may result from age. *S. microphthalma* is characterised by the possession of eyes which the upper half shows two terminal facets only. The species of the group are widely distributed in sub-tropical and tropical oceans.

GROUP C.

Species with the elongate limbs terminating in real chelae formed by the opposition of a stiff curved spine from the end of the last segment with a stiff curved spine which is fused to the end of the penultimate segment. There are no long accessory setae on either segment although small ones may be present. (See figures in Sars 1885, Hansen 1910, and Banner 1950.) There is no spur on the antepenultimate segment.

The two species are separated by differences in the eyes, in the copulatory organs and in the dorsal armature of the fourth and fifth abdominal segments as follows:

A. Eyes in adults and sub-adults with the upper section much smaller than the lower. The fourth and fifth abdominal segments each with a conspicuous dorsal median tooth from the mid-hind margin.

Stylocheiron abbreviatum Sars 1885.

Distribution: Tropical and sub-tropical oceans. For descriptions and figures see Sars (1885); and Hansen (1910), and (1912). For references, Tattersall (1939).

AA. Eyes in adult and sub-adults with upper section little smaller than the lower. The fourth and fifth abdominal segments with no dorsal tooth.

Stylocheiron maximum Hansen 1908.

Distribution: Tropical and sub-tropical oceans. For descriptions and figures see Hansen (1908), (1910), (1912); and Banner (1950), who includes a detailed discussion of the variations in the copulatory organ.

E. The Distribution of the Euphausiacea.

(Tables 1-9, Figs. 1-3.)

1. GENERAL DISTRIBUTION.

(Tables 1-2, Figs. 1-3.)

The members of the order are marine and pelagic. As is the case with all such organisms sampling is difficult and costly. In consequence knowledge of distribution of the species is not extensive even in such regions as the North Atlantic, and the Antarctic, where great fisheries exist on fish and whales which are dependent largely on the Euphausiacea. In areas where lesser fisheries exist, or where fisheries are based less manifestly on Euphausiid species, knowledge of that group is sketchy, and has been gathered for the most part during global voyages of oceanographical expeditions. Sufficient information exists, however, to permit some general analysis of species distribution. When this analysis is made, it is apparent that Euphausiacean species are zoned within broader or narrower ocean limits, and that it is possible to present their world distribution in a schematic form in terms of geographic zones, as well as in terms of oceans (Tables 1 and 2; Figs. 2 and 3), although the species are in many cases more nearly tied to the water masses and major current systems of the oceans (see Fig. 1 for comparison). The schematic distributions indicated in the tables and figures give the areas where the species may be regarded as constituting normal elements of the zoo-plankton. This method of representation is two-dimensional and it ignores the layering with depth which appears to be a characteristic of some species as recorded by vertical plankton hauls. In this respect such a vertical section of species distribution in the North Atlantic as is given by Einarsson (1945, fig. 63), although schematic, is essential to an understanding of the general distributional picture.

The adults of sub-tropical and tropical species may be taken over a wide temperature range but this narrows sharply as higher latitudes are reached (Tables 8 and 9). There is some evidence from the work of Einarsson (1945), Fraser (1936), John (1936), and in Tables 8 and 9 of this report (see Section E. 3. c), that the spawning temperature ranges, and those of the larvae, lie within narrower limits.

In the case of *Nyctiphanes australis* the observed range of the species is from 10° C. to 23° C. In order to test the effects of a temperature rise on the survival rate of individuals a small scale experiment was carried out at Ulladulla, New South Wales, in October, 1943, at a period of surface swarming of adult males. Of sixty adult males which were collected in one haul, thirty were placed in each of two shallow containers containing sea-water from the surface layer at 16° C. One of these was kept at 16° C. within limits of 1°C. The other was raised to 23° C. over a period of two hours, and maintained at that temperature. Specimens were removed as they died. All specimens in the tank 16° C. were dead after 22 hours, in the 23° C. tank after 21 hours. There was no significant difference in the mortality curve from either sample. It is thus possible that the temperature tolerances of adult individuals of this species approximate that of the species itself in the upper temperature ranges.

Experiments of this nature are difficult to carry out in small fishing boats, but in February, 1952, an attempt was made to find the lethal temperatures of adults of *Euphausia recurva* off Rottnest Island, Western Australia. Only 12 identifiable adult males were collected. Of these six were placed in each of two large shallow glass jars of sea-water at the collecting temperature, 24° C. The jars were suspended in containers containing sea-water at the collecting temperature. Air, at a low pressure, was bubbled into each jar. The second container was slowly heated. After 30 minutes, when the temperature in the suspended jar had reached 33° C., the six specimens suddenly lost their typical transparency and became very slightly translucent, within a minute their appendages had ceased moving and the animals rapidly became translucent and then opaque. The experiment was inconclusive as after 45 minutes the six specimens in the unheated control jar the temperature of which had risen only 1° C. passed through the same phases. The distributional temperature range of the adults of this species is 15° C. to 26° C. (Table 9).

No further specimens were taken. In any case experimentation on temperature adaptation and lethal temperatures of plankton organisms which is involved in the problem of temperature control of distribution is best essayed in research vessels with a laboratory equipped for that purpose.

Figs. 2 and 3, using a well-known device, show the species distribution in five genera *(Euphausia, Meganyctiphanes, Nyctiphanes, Pseudeuphausia, Thysanoessa)*. It is noteworthy that speciation in the genus *Euphausia* is most evident in tropical waters; but an examination of the zonal distribution of the species of genus (fig. 2) reveals that extensive speciation together with a progressive replacement of the species occurs also in antarctic, sub-antarctic, and sub-tropical regions. In the northern hemisphere the only species penetrating into arctic waters occurs in the North Pacific, viz., *Euphausia pacifica*. This position is reversed in the case of *Thysanoessa,* which has no tropical representatives but which is well represented in the cooler waters of the northern hemisphere and poorly in the southern hemisphere (fig. 3); in this case *T. gregaria* with spawning ranges in both sub-tropical oceans may be a connecting species at a depth in tropical oceans.

A limitation on the study of the Order has been the very great difficulty of maintaining stations so sited as to give a continuous picture of the seasonal activity of even common and accessible species. Even the very

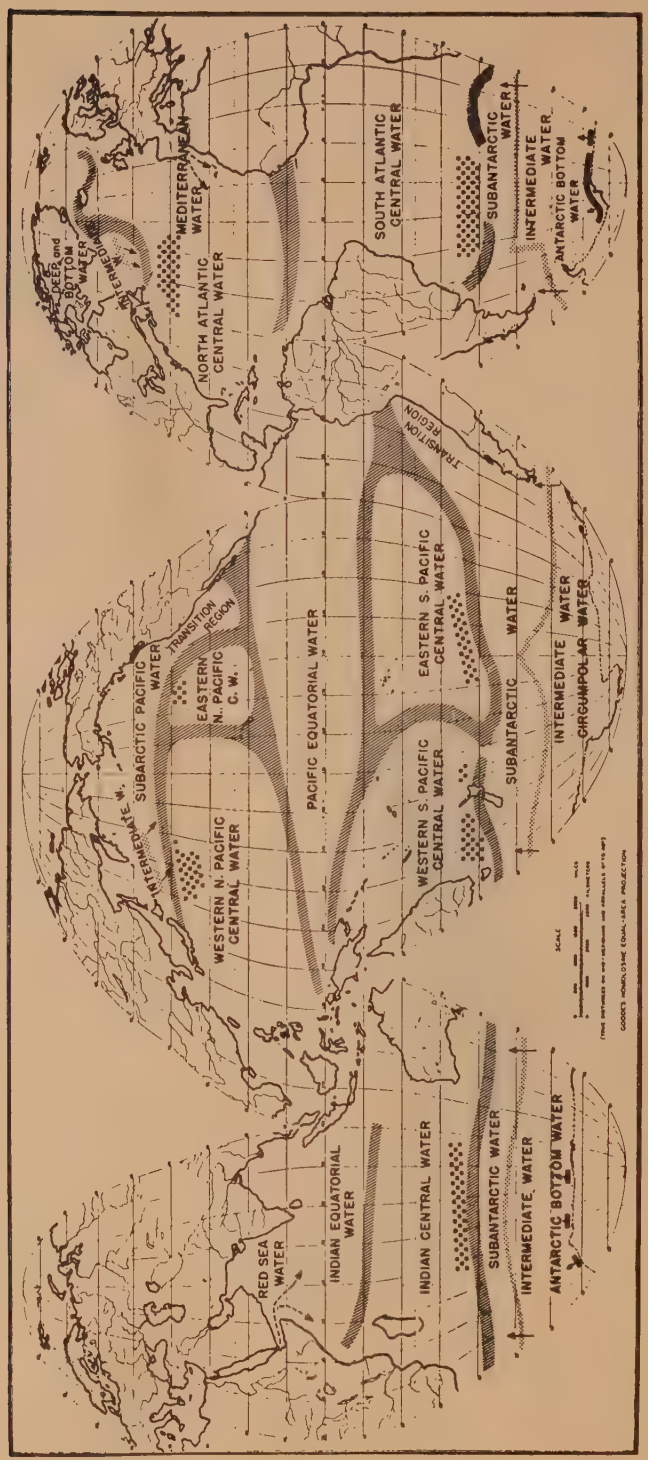


Fig. 1. Water masses of the oceans. (After Sverdrup, Johnson, and Fleming, 1942.)

thorough studies by Discovery Committee workers in the Southern Ocean, and by Einarsson in the North Atlantic, are based on stations greatly separated in space, and with irregular time intervals. Direct as opposed to inferential evidence will be obtained on this and on other characteristics of the species of the Order only when continuous oceanic stations can be maintained within a very limited area. When the seasonal pattern of distribution of various species is known it should be possible to define distributional limits more strictly.

In spite of the nature of the present data it is obvious that many of the species occupy characteristic oceanic water masses and current systems. It is probable, thus, that isolating physiological differences are present. In any case the various patterns of petasma and thyleca characteristic of the taxonomic species suggest some form of a lock and key, isolating, reproductive mechanism.

TABLE 1.

EUPHAUSIACEA

Oceanic Distribution

Species	East Atlantic	West Atlantic	East Pacific	West Pacific	East Indian	West Indian
BENTHEUPHAUSIA						
amblyops Sars 1883		x	x		x	x
Number of Species, 1		1	1		1	1
THYSANOPODA						
acutifrons H. & T. 1905	x	x				
microphthalma Sars 1883		x				
egregia Hansen 1905		x				
obtusifrons Sars 1883	x		x	x		x
orientalis Hansen 1910	x	x		x	x	x
pectinata Ortmann 1893	x	x	x	x	x	x
aequalis Hansen 1905	x	x	x	x	x	x
monocantha Ortmann 1893		x	x	x	x	x
cornuta Illig 1905		x	x	x		
tricuspidata Milne-Edwards 1830	x	x	x	x	x	x
cristata Sars 1883		x	x			
johnstoni Sheard 1942				x	x	
dubia Banner 1950			x			
Number of Species, 13	6	10	8	8	6	6
MEGANYCTIPHANES						
norvegica (M. Sars) 1857	x	x				
Number of Species, 1	1	1				
NYCTIPHANES						
couchii Bell 1853	x					
simplex Hansen 1911			x			
africana Zimmer 1912	x					
capensis Hansen 1911						x
australis Sars 1883				x	x	
Number of Species, 5	2		1	1	1	1
PSEUDEUPHAUSIA						
latifrons Sars 1883				x	x	x
colosii Torelli 1934						R
Number of Species, 2						
EUPHAUSIA						
krohnii (Brandt) 1851	x	x				
americana Hansen 1911		x				
messanensis Colosi 1916	M					
pacifica Hansen 1911			x	x		
brevis Hansen 1905		x	x	x		x
recurva Hansen 1905	x		x	x	x	x
hemigibba Hansen 1910	x	x			x	x
mutica Hansen 1905	x	x	x	x	x	x
gibboides Ortmann 1893		x	x			x
tenera Hansen 1905	x	x	x	x	x	x
hanseni Zimmer 1915	x					
paragibba Hansen 1910			x		x	x
pseudogibba Ortmann 1893	x		x	x	x	x
eximia Hansen 1911			x			
diomedeae Ortmann 1894			x	x	x	x
lamelligera Hansen 1911	?x		x			
distinguenda Hansen 1911			x			x
sibogae Hansen 1905				x	x	
fallax Hansen 1916				x		
alvae Boone 1935				x		
consuelae Boone 1935				x		
mucronata Sars 1883			x			
sanzoi Torelli 1934						R

Species	East Atlantic	West Atlantic	East Pacific	West Pacific	East Indian	West Indian
EUPHAUSIA						
gibba Sars 1883			x	x		
spinifera Sars 1883	x	x	x	x	x	x
similis Sars 1883	x	x	x	x	x	x
similis var. armata Hansen	x	x	x	x	x	x
lucens Hansen 1905	x	x	x	x	x	x
longirostris Hansen 1908	x	x	x	x	x	x
vallentini Stebbing 1900	x	x	x	x	x	x
triacantha H. & T. 1906	x	x	x	x	x	x
frigida Hansen 1911	x	x	x	x	x	x
superba Dana 1850	x	x	x	x	x	x
crystallorophias H. & T. 1905	x	x	x	x	x	x
Number of Species, 34	18	17	24	22	18	21
TESSARABRACHION						
occulatum Hansen 1911				x		
Number of Species, 1				1		
THYSANOESSA						
raschii (M. Sars) 1864	x	x				
inermis (Kroyer) 1846	x	x	x			
longicaudata (Kroyer) 1846	x	x				
longipes Brandt 1951			x	x		
spinifera Holmes 1900			x			
parva Hansen 1905	x	x				
gregaria Sars 1883	x	x	x	x	x	x
vicina Hansen 1913	x	x	x	x	x	x
macrura Sars 1883	x	x	x	x	x	x
Number of Species, 9	7	7	6	4	3	3
NEMATOSCELIS						
megalops Sars 1883	x	x				?x
atlantica Hansen 1910	x	x				
microps Sars 1883	x	x	x	x	x	x
tenella Sars 1883	x	x	x	x	x	x
lobata Hansen 1916				x		
gracilis Hansen 1910			x	x	x	x
difficilis Hansen 1911				x		
Number of Species, 7	4	4	3	5	3	3
NEMATOBRACHION						
boopis Calman 1896	x	x	x	x	x	x
flexipes Ortmann 1893	x	x	x	x	x	x
sexspinosus Hansen 1911	x		x			
Number of Species, 3	3	1	3	2	1	2
STYLOCHEIRON						
maximum Hansen 1908	x	x	x	x	x	x
longicorne Sars 1883	x	x	x	x	x	x
carinatum Sars 1883	x	x	x	x	x	x
suhmii Sars 1883	x		x	x		
elongatum Sars 1883	x	x	x	x		x
abbreviatum Sars 1883	x	x	x	x	x	x
affine Hansen 1910			x	x	x	x
insulare Hansen 1910					x	
microphthalma Hansen 1910			x		x	
armatum Colosi, 1917		x				x
Number of Species, 10	6	6	8	7	7	7
Total Number of Species, 86	47	47	54	51	41	46

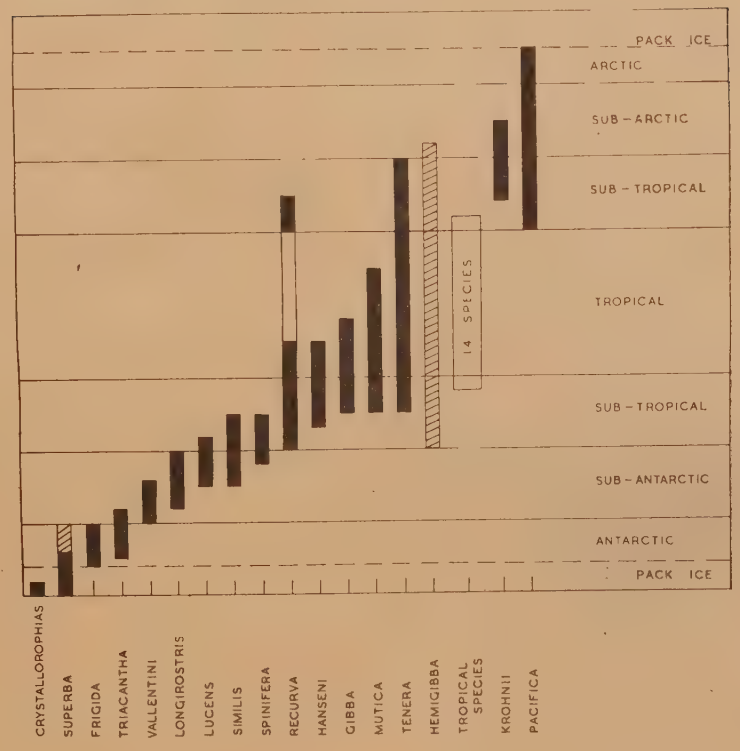


Fig. 2. Schematic distribution of the genus Euphausia in terms of geographic zones.

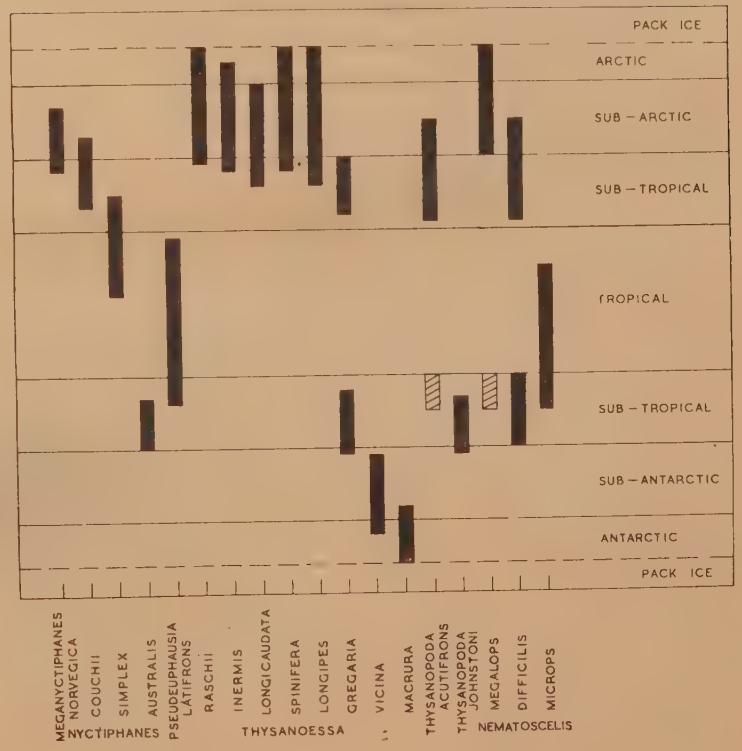


Fig. 3. Schematic distribution of some Euphausiid species in terms of geographic zones.

TABLE 2.

EUPHAUSIACEA

Distribution in Conventional Geographic Zones

Species	Arctic	Subarctic	North Subtropical	Tropical	South Subtropical	Subantarctic	Antarctic
BENTHEUPHAUSIA							
amblyops Sars 1883			x	x	x		
Number of Species, 1			1	1	1		
THYSANOPODA							
acutifrons H. 7 T. 1905		x	x				
microphthalma Sars 1883			x				
egregia Hansen 1905			x	x			
obtusifrons Sars 1883			x	x	x		
orientalis Hansen 1910			x	x	x		
pectinata Ortmann 1893			x	x	x		
aequalis Hansen 1905			x	x	x		
monocantha Ortmann 1893			x	x	x		
cornuta Illig 1905			x	x	x		
tricuspidata Milne-Edwards 1830				x			
cristata Sars 1883							
johnstoni Sheard 1942					x	x	
dubia Banner 1950		x	x				
Number of Species, 13		2	10	9	7	1	
MEGANYCTIPHANES							
norvegica (M. Sars) 1857		x	x				
Number of Species, 1		1	1				
NYCTIPHANES							
couchii Bell 1853			x				
simplex Hansen 1911			x	x			
africana Zimmer 1912					x		
capensis Hansen 1911					x		
australis Sars 1883					x		
Number of Species, 5			2	1	3		
PSEUDEUPHAUSIA							
latifrons Sars 1883			x	x	x		
colosii Torelli 1934				x			
Number of Species, 2			1	2	1		
EUPHAUSIA							
krohnii (Brandt) 1851			x				
americana Hansen 1911			x	x			
messanensis Colosi 1916			x				
pacifica Hansen 1911			x				
brevis Hansen 1905			x	x	x		
recurva Hansen 1905			x	x	x		
hemigibba Hansen 1910			x	x	x		
mutica Hansen 1905			x	x	x		
gibboides Ortmann 1893			x	x	x		
tenera Hansen 1905				x	x		
hanseni Zimmer 1915				x	x		
paragibba Hansen 1910				x			
pseudogibba Ortmann 1893				x			
eximia Hansen 1911			x	x			
diomedeae Ortmann 1894				x			
lamelligera Hansen 1911				x			
distinguenda Hansen 1911				x			
sibogae Hansen 1905				x			
fallax Hansen 1916				x			
alvae Boone 1935				x			
consuelae Boone 1935				x			
mucronata Sars 1883				x			

Species	Arctic	Subarctic	North Subtropical	Tropical	South Subtropical	Subantarctic	Antarctic
EUPHAUSIA							
sanzoi Torelli 1934				x			
gibba Sars 1883			x	x	x		
spinifera Sars 1883					x		
similis Sars 1883			x	x	x	x	
similis var. armata Hansen					x	x	
lucens Hansen 1905					x	x	
longirostris Hansen 1908						x	
vallentini Stebbing 1900						x	
triacantha H. & T. 1906						x	x
frigida Hansen 1911							x
superba Dana 1850							x
crystallorophias H. & T. 1905							x
Number of Species, 34			10	22	12	6	4
TESSARABRACHION							
occulatum Hansen 1911		x	x				
Number of Species, 1		1	1				
THYSANOESSA							
raschii (M. Sars) 1864	x	x					
inermis (Kroyer) 1846	x	x					
longicaudata (Kroyer) 1846		x	x				
longipes Brandt 1851		x	x				
spinifera Holmes 1900		x	x				
parva Hansen 1905			x				
gregaria Sars 1883			x	?x	x		
vicinia Hansen 1913						x	
macrura Sars 1883							x
Number of Species, 9	2	5	5		1	1	1
NEMATOSCELIS							
megalops Sars 1883		x	x		?x		
atlantica Hansen 1910			x				
microps Sars 1883			x	x	x		
tenella Sars 1883				x			
lobata Hansen 1916				x			
gracilis Hansen 1910				x			
difficilis Hansen 1911			x		x		
Number of Species, 7		1	4	4	2		
NEMATOBRACHION							
boopis Calman 1896			x	x	x		
flexipes Ortmann 1893			x	x	x		
sexspinosus Hansen 1911			x	x			
Number of Species, 3			3	3	2		
STYLOCHEIRON							
maximum Hansen 1908			x	x	x		
longicorne Sars 1883			x	x	x		
carinatum Sars 1883			x	x	x		
suhmii Sars 1883			x	x	x		
elongatum Sars 1883			x	x	x		
abbreviatum Sars 1883			x	x	x		
affine Hansen 1910				x			
insulare Hansen 1910				x			
microphthalma Hansen 1910				x			
armatum Colosi 1917				x			
Number of Species, 10			6	10	6		
Total Number of Species, 86	2	8	44	52	35	7	5

2. EUPHAUSIACEA OF THE B.A.N.Z.A.R.E. STATIONS.

(Table 3.)

As stated earlier, there is little point in anticipating the findings of workers on the Euphausiacea with access to the extensive "Discovery" material from the antarctic and sub-antarctic regions, particularly as extensive analyses of this material are in progress. The B.A.N.Z.A.R.E. records of Euphausiacea (Table 3) are scanty, and are given here in order that they may be incorporated in the final summary. Some associated data are given in the table; the remainder may be obtained from the Biological Organization and Station List published as Volume I, part 1, of the B.A.N.Z.A.R.E. Reports, Series B. In the antarctic itself, the plankton stations lay between Enderby Land and Scott Island, and it is noteworthy that *Thysanoessa macrura* was by far the predominate Euphausiid of this area with *Euphausia superba* in the minority. For the genus *Euphausia* the distribution followed the accepted pattern (John, 1936).

An interesting addition to the southern faunal list is *Nematoscelis megalops* in the Southern Indian Ocean in latitude 38° 33′ S., longitude 109° 22′ E.

TABLE 3.

EUPHAUSIID DISTRIBUTION

B.A.N.Z. Antarctic Research Expedition, 1929-1931

Species	Station Number	Depth (Metres)	Temperature Range		Salinity Range	
			Max. °C.	Min. °C.	Max.	Min.
Thysanoessa macrura	22	50–0	—0·77	—1·22	33·9	33·8
	22	170–0	1·26	—0·77	34·5	33·8
	22	500–250	1·96	1·26	34·6	34·5
	23	100–0	(—1·0)		(33·9)	
	24	100–50	—1·28	—1·43	34·3	34·0
	24	135–0	—0·75	—1·3	34·3	33·9
	25	100–0	(—1·3)		(33·9)	
	28	130–0	—0·72	—1·6	34·3	33·6
	28	50–0	—0·72	—1·51	34·2	33·7
	28	100–50	—1·57	—1·67	34·3	34·2
	28	750–510	—0·43	—0·45	34·7	34·6
	30	100–50	—1·65	—1·69	34·4	34·0
	30	176–0	—0·67	—1·5	34·4	33·9
	31	91–0	—0·88	—1·7	34·3	33·8
	31	100–50	—1·7	—1·7	34·3	34·3
	33	50–0	—0·6	—1·5	34·1	33·9
	33	125–0	—0·56	—1·6	34·3	33·4
	33	500–250	0·0	—1·7	34·5	34·4
	35	1600				
	37	50–0	—0·04	—0·9	33·9	33·8
	37	147–0	—0·04	(—1·6)	(34·2)	33·8
	41	130–0	—0·7	—1·5	33·6	33·6
	43	50–0	0·1	—1·3	34·1	33·8
	43	100–50	—1·3	—1·6	34·2	34·1
	43	250–100	0·7	—1·6	34·6	34·2
	43	169–0	0·12	—1·3	34·2	33·8
	44	50–0	0·1	—1·1	34·0	33·7
	44	100–50	—1·0	—1·1	34·3	34·0
	44	250–100	1·2	—1·0	34·6	34·3
	44	750–500	1·3	1·0	34·7	34·6
	45	50–0	—1·0	—0·8	34·0	33·8
	45	100–50	—0·8	—1·0	34·2	34·0
	45	100–0	1·0	—1·0	34·2	33·8
	45	250–0	1·0	—1·4	34·7	33·8
	45	250–100	—1·4	—1·0	34·7	34·2
	45	1000–750	1·4	1·2	34·8	34·7
	46	50–0	2·1	2·0	33·9	33·9
	46	250–100	1·8	0·5	34·4	34·0
	46	750–500	2·1	2·1	34·7	34·6
	93	1500				
	96	93	(—1·3)			(33·4)
Thysanoessa vicina	65	128–0	5·6	4·2	33·8	33·7
Thysanoessa gregaria	67	90–0	(10·8)		(34·2)	
	68	85–0	8·6	8·3	34·0	34·0
	73	112–0	(15)			(34·9)
Euphausia crystallorophias	33	125–0	—0·56	—1·6	34·3	33·4
	93	1500				

TABLE 3 (continued).

Species	Station Number	Depth (Metres)	Temperature Range Max. °C.	Temperature Range Min. °C.	Salinity Range Max.	Salinity Range Min.
Euphausia superba	24	1000–750	1·27	0·93	34·7	34·6
	30	176–0	—0·67	—1·5	34·4	33·9
	31	91–0	—0·88	—1·7	34·3	33·8
	33	125–0	—0·56	—1·6	34·3	33·4
	38	1000–750	0·1	—1·0	34·6	34·5
	45	100–0	1·0	—1·0	34·2	33·8
	45	750–500	1·5	1·4	34·7	34·7
	93	2260–0				
	102	750–0	—0·1	—0·99	34·5	32·8
Euphausia triacantha	65	500–250	3·0	2·7	34·4	33·8
	65	750–500	2·7	2·6	34·5	34·4
	93	1500				
	96	93	(—1·3)			(33·4)
Euphausia frigida	23	100–0				
	46	250–100	1·8	0·5	34·1	34·0
	46	500–250	2·1	1·8	34·6	34·4
	65	250–100	4·2	2·7	33·8	33·8
	65	500–250	3·0	2·6	34·4	33·8
Euphausia longirostris	67	90–0	(10·8)		(34·2)	
	67	2000				
	68	85–0	8·64	8·3	34·0	34·0
	111	1700				
Euphausia vallentini	65	500–250	3·0	2·6	34·4	33·8
	65	750–500	2·7	2·6	34·5	34·4
	67	2000				
	68	85–0	8·64	8·3	34·0	34·0
Euphausia lucens	73	112–0	(15)		(34·9)	
Euphausia similis	67	2000				
	73	112–0	(15)		(34·9)	
Euphausia var. armata	111	1700				
Euphausia spinifera	73	112–0	(15)		(34·9)	
Nematoscelis megalops	73	112–0	(15)		(34·9)	
Stylocheiron sp.	67	2000				
	73	112–0	(15)		(34·9)	

3. EUPHAUSIACEA OF THE WESTERN SOUTH PACIFIC.

(Tables 4-9.)

The results of the plankton studies of the Great Barrier Reef Expedition in latitude 15°-17° S.; isolated plankton hauls from various sources, notably those taken by the late Surgeon Commander Paradyce between 16° S. and 45° S.; the eastern plankton hauls of the B.A.N.Z.A.R.E. from latitude 40° S. to 65° S.; together with the published records in the "Terra Nova" and "Discovery" Reports relating to latitude 40° S. to 65° S. combined with the Eastern Australian material collected for the purpose of this report, have enabled a study to be made of the distribution and temperature relations of the Euphausiacea within the area extending between latitudes 15° S. and 65° S. and bordered by longitudes 145° E. and 155° E. The results are summarized in Tables 4-9.

(a) SOUTH-EASTERN AUSTRALIAN "WARREEN" STATIONS.

(Tables 4-5.)

The plankton programmes of F.R.V. "Warreen" in south-eastern Australian coastal and slope waters were carried out as accessories to the hydrological programmes and both were at times interrupted by fisheries investigations. Consequently, although approximately 1,100 plankton samples were included from the traverses which were made between 1938 and 1942, their chief value as regards the Euphausiacea was to indicate the distribution ranges and the approximate temperature relations of the species, in addition to providing material for the analysis of larval development. Analysis of detailed distribution, and of seasonal and yearly fluctuations in the zooplankton, can be based only on rigorous, continued sampling. This could not be expected in terms of the general programme of F.R.V. "Warreen," and analysis of the material confirmed this belief with regard to the Euphausiacea. Some useful observations were made, however, on those subjects, particularly with regard to *Nyctiphanes australis*, and these, incorporated with the results of later investigations, are examined later in this section.

Tables 4 and 5 present an outline of species distribution which was confirmed by surveys subsequent to 1942. The species distributions listed in those tables are incorporated in Tables 8 and 9. Some points not brought out in the tables are of importance. These are as follows:

(i) The species *Nyctiphanes australis* and *Pseudeuphausia latifrons* were not found together, although at times one was found within the range of the other, the maximum interpenetration being about 4° of latitude. As far as can be judged from the samples the replacement process is a slow one, e.g., *Pseudeuphausia latifrons* was not present between latitudes 31-34° S. during 1938 and 1939, but appeared there in 1940-41, again giving place to *Nyctiphanes australis* until at least 1945.

(ii) There was some lateral displacement of species, this with no marked rhythm. Slope and ocean species, such as *Nematoscelis difficilis* at times invaded shelf waters in large swarms, tow-nettings containing many developmental phases. In such a cases, the coastal species, *Nyctiphanes australis,* was not a prominent member of the zooplankton of the deeper shelf waters in any phase, but appeared to be concentrated in shallower waters. It is possible that the effect was due to irregular lateral or oblique shifts of slope or ocean water masses.

(iii) Various species of the genus *Thysanopoda,* e.g., *T. monocantha, orientalis, obtusifrons, aequalis, pectinata* and *johnstoni,* have appeared in the plankton in very small numbers from time to time, chiefly in the deeper hauls at slope and ocean stations. The main occurrences were during 1939. They have not been included in Tables 4 and 5, but are shown in Table 9.

TABLE 4.

EUPHAUSIID SPECIES IN ALL PLANKTON NET HAULS

"Warreen" Traverses, South West Pacific Ocean

Eastern Australian Coastal Shelfs (on-shore stations), 1938-1942

Latitude	Times Observed															
	N. australis	P. latifrons	E. recurva	E. spinifera	E. similis var. armata	E. similis	E. lucens	E. gibba	E. tenera	E. mutica	N. difficilis	N. microps	T. gregaria	S. carinatum	S. abbreviatum	No. of hauls examined
45° S. to 42° S.	12	—	—	—	1	2	1	—	—	—	2	—	3	—	—	43
42° S. to 39° S.	21	—	1	—	—	—	—	—	—	—	2	—	3	—	—	39
39° S. to 37° S.	29	—	5	—	—	—	—	—	—	—	2	—	8	—	—	71
37° S. to 35° S.	31	—	6	—	—	—	—	—	—	—	2	—	12	—	1	74
35° S. to 33° S.	79	3	12	—	—	—	—	—	—	—	9	—	11	—	1	158
33° S. to 31° S.	4	3	3	—	—	—	—	—	—	—	1	—	1	—	1	24
31° S. to 29° S.	1	7	4	—	—	—	—	—	—	—	4	—	2	1	—	39
29° S. to 27° S.	—	8	2	—	—	—	—	—	—	—	—	—	—	2	—	26
27° S. to 24° S.	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	28
Totals	177	25	33	—	1	2	1	—	—	—	22	—	40	3	3	502

TABLE 5.

EUPHAUSIID SPECIES IN ALL PLANKTON NET HAULS

"Warreen" Traverses, South West Pacific Ocean

Eastern Australian slope waters (off-shore stations), 1938-1942

Latitude	Times Observed															
	N. australis	P. latifrons	E. recurva	E. spinifera	E. similis var. armata	E. similis	E. lucens	E. gibba	E. tenera	E. mutica	N. difficilis	N. microps	T. gregaria	S. carinatum	S. abbreviatum	No. of hauls examined
45° S. to 42° S.	1	—	—	4	4	5	1	—	—	—	8	—	7	1	—	48
42° S. to 39° S.	—	—	3	7	5	1	1	—	—	—	8	—	7	6	2	41
39° S. to 37° S.	2	—	14	6	5	4	—	—	—	—	4	—	12	3	—	63
37° S. to 35° S.	3	1	16	11	5	3	—	1	—	—	11	—	13	—	—	73
35° S. to 33° S.	6	—	55	6	3	8	—	13	1	2	33	7	38	17	9	127
33° S. to 31° S.	—	2	4	—	—	—	—	1	—	—	3	2	11	3	1	22
31° S. to 29° S.	—	—	11	—	—	—	—	1	—	—	5	1	3	4	2	39
28° S. to 27° S.	—	1	1	—	—	—	—	—	—	—	—	—	—	2	—	30
27° S. to 24° S.	—	2	2	—	—	—	—	—	2	—	—	—	1	2	—	9
Total	12	6	106	34	22	21	2	16	3	2	72	10	92	38	14	452

(b) R.R.S. "DISCOVERY II" TRAVERSES, OCTOBER, 1950.

(Table 6.)

During October, 1950, two 200-mile traverses, one easterly along latitude 37° S., the other easterly along latitude 34° S., were made by R.R.S. "Discovery II" on behalf of C.S.I.R.O., Division of Fisheries. The general results of the hydrology and plankton tows will be published elsewhere but the distribution of the Euphausiacea from the N 100 B. tows is given here (Table 6). The shelf stations of these traverses were 2706, 2707, 2725 and 2724; the slope stations were 2708 and 2723; the remainder were ocean stations. The table illustrates the changes in the species associations which occur in passing from the warmer sub-tropical waters to the cooler, although the conditions recorded for the 34° traverse are somewhat more typical of areas more northerly of this latitude. The presence of *Euphausia gibba* and *E. recurva* in the same hauls, and the absence of *Nyctiphanes australis* at shelf station 2725 are suggestive of somewhat more tropical conditions in that area.

TABLE 6.

EUPHAUSIACEA

R.R.S. "Discovery II", N.S.W. Traverse, October, 1950

Station and Time	Long. ° E.	Nyctiphanes australis	Thysanoessa gregaria	Nematoscelis difficilis	Stylocheiron carinatum	Stylocheiron abbreviatum	Euphausia recurva	Euphausia mutica	Euphausia tenera	Euphausia gibba	Euphausia similis	Euphausia similis var. armata	Euphausia spinifera	Thysanopoda johnstoni	Thysanopoda monacantha
(a) *Latitude* 34° *S.*															
2725 night	151° 24′		x	x	x		xxx			xxx					
2724 night	151° 25′		x	x	x		xxx								
2723 day	151° 33′		x	x	x	x	x								
2722 day	151° 45′		x	x	xxx			xxx							
2721 day	152° 03′		x	x	x										x
2720 day	152° 27′		xx	x	xx										
2719 day	152° 38′		x	x	xxx		xxx								xxx
2718 night	153° 02′		x	xxx	xxx		xxx	xx	xx	xxx				xxx	
2717 day	154° 16′		x	x	x		xxx								
2716 night	155° 18′														
(b) *Latitude* 37° *S.*															
2706 day	150° 10′	xx	x												
2707 day	150° 17′	xxx	x												
2708 day	150° 24′	x	x	x			x				x		x		
2709 night	150° 35′		x	x	x		xxx				x	xxx	xxx		
2710 night	150° 48′		xx				xxx					xxx	xxx		
2711 night	150° 13′		x	x			xx				xx	xxx	xxx		
2712 day	151° 33′		xxx	xxx											
2713 day	151° 55′		x	x		x									
2714 night	153° 04′		xx	xx	x						xx		x		
2715 day	154° 05′		x	x			x								

Key: xxx = Series of growth stages present. xx = One growth stage present. x = Few specimens present.

(c) THE DISTRIBUTION OF *NYCTIPHANES AUSTRALIS*.

(Table 7.)

The occurrence of *Nyctiphanes australis* in a high proportion of the plankton hauls which were made within the range 31° S. to 43° S. latitudes, often in very large swarms including many developmental phases, has enabled some analysis to be made of the temperature distribution relations of the species. These are given in Table 7 where the coastal hauls for which temperature data are available, and which have been taken over the known range of the species (398 samples), have been analysed in terms of latitude and temperature. The data have been insufficient to warrant a breakdown of the occurrence of the species into latitude sub-ranges and temperatures; but the general impression that has been gained during the course of the field-work and analysis of the hauls, and from the examination of fish stomach-contents, is that the optimal latitudinal range is 34° S. to 42° S. and the optimal temperature range is from 12° C. to 18° C. This impression is strengthened when section (d) of Table 6 is examined.

A further point which suggests that the optimal temperature range lies between 12° C. and 18° C. is that no individuals have been found within these limits bearing external parasites of the family Ellobiosidae

(*Amallocystis* sp.), yet at temperatures both below and above these limits infected specimens are to be found. (The parasite attached dorsally to the carapace of the host.) The parasite itself is apparently capable of flourishing over the whole temperature range of *N. australis* as infected slope and ocean species such as *N. difficilis, E. recurva* and *T. gregaria* have been taken in company with uninfected *N. australis* in coastal waters at the intermediate temperatures. The observation suggests that infection of this type may be a result of lack of vitality in the organism and that this may be correlated with unsuitable living conditions of one kind or another. The subject is one which requires further investigation, but it invites the speculation that a study of host-parasite relationships in marine animals in general might indicate some types of parasitism which may be of value in showing the limits of various types of marine ecological boundaries.

TABLE 7.

NYCTIPHANES AUSTRALIS

Adults and Larvae

Temperature Distribution, Latitudes 43° S. to 31° S.
"Warreen" Traverses, Eastern Australian Continental Shelf

(a) *Temperature Intervals*	11° C.	13° C.	15° C.	17° C.	19° C.	21° C.
Latitude Range 43°-42° S., Hauls	16	29	3			
Latitude Range 42°-39° S., Hauls	9	10	24	1		
Latitude Range 39°-37° S., Hauls		21	15	11	7	
Latitude Range 37°-35° S., Hauls		2	23	15	15	
Latitude Range 35°-33° S., Hauls		7	64	68	33	13
Latitude Range 33°-31° S., Hauls			5	5	1	1
Number of hauls between 43° and 31° S.	25	69	134	100	56	14
(b) Number of times *N. australis* observed	8	21	57	67	26	9
(c) Percentage of times observed		30	42	67	45	
(d) Temperature distribution of growth stages						
Adult ♂♂ Times observed	4	10	28	27	12	1
Adult ♀♀ Times observed	4	10	29	27	10	1
Ovigerous ♀♀ Times observed	1	3	12	7	4	
Adolescent Times observed	4	8	21	20	5	1
Post-larva Times observed	3	8	24	24	7	1
Furcilia Times observed	1	11	41	45	19	7
Calyptopis Times observed	1	10	30	24	15	4

(d) EUPHAUSIACEA OF THE EASTERN AUSTRALIAN CONTINENTAL SHELF.

(Table 8.)

The available observations, including those given in Tables 3 to 6, have been summarized in Table 8, which lists the latitude range, temperature range, and occurrences of the adult and larval phases of the species. Two species (*N. australis* and *P. latifrons*) are restricted to shelf waters; but three other species (*N. difficilis, T. gregaria,* and *E. recurva*), normally ocean and slope inhabitants, are also common in all stages at times. The remaining species are quite rare visitants.

During the course of the examination of the plankton samples and records from the waters of the continental shelf extending from latitudes 14° S. to 44° S. the occurrence of other planktonic crustacea (notably the Hyperiid Amphipods, Decapod larvae, and Cladocera) was noted. These observations support the inference which could be drawn from the distribution of *N. australis* and *P. latifrons,* that the continental shelf might be regarded as consisting of two major faunal areas, a warm sub-tropical region, typified by the occurrence of *P. latifrons;* and a cool sub-tropical region, typified by the occurrence of *N. australis;* with the division a shifting band, lying approximately between latitudes 30° S. and 34° S.

(e) OCEANIC DISTRIBUTION LAT. 15° S. TO 65° S., LONG. 145° E. to 155° E.

(Table 9, and see Figs. 2 and 3.)

In this oceanic sector, 8 out of the 9 known genera, and 37 out of the 86 known species of the Euphausiidae have been collected, 16 of the species in very large numbers. The remainder (chiefly tropical, or bathyplanktonic species) have been rare inclusions in the plankton hauls. Of the 16 common species, 6 species are known to be of major importance in fisheries economy. These are *Euphausia superba* and *Thysanoessa macrura* in Antarctic whaling; *Nyctiphanes australis, Thysanoessa gregaria, Euphausia recurva* and *Nema-*

toscelis difficilis in various sub-tropical Australian fisheries. In the cooler part of the sub-tropical region two additional species, *Euphausia spinifera* and *E. similis*, may well be found to play an important part in the off-shore distribution of the southern bluefin tuna, and of the striped tuna. A general consideration of Table 9 indicates that regional faunal associations of the type suggested by the study of the eastern Australian coastal shelf occur also in the adjacent ocean waters, the actual zone of demarcation between the cool and warmer associations shifting from year to year, and perhaps season to season, with latitudes in the vicinity of 34° S. as a mean boundary. It must be emphasized, however, that the rigorous and continuous sampling in ocean waters necessary to delimit this boundary has not been carried out. The mapping of this fluctuating faunal boundary yearly would be of assistance in explaining the otherwise puzzling fluctuations in the distribution of the pelagic fishes of the cooler sub-tropical area along the New South Wales coast (see Sheard 1949, Figs. 1 and 2, and Table 6; Blackburn and Tubb 1950; and Sheard 1950).

TABLE 8.

EUPHAUSIACEA

Eastern Australian Continental Shelf, Latitude 15° S. to 44° S.
"Warreen" Traverses, South-West Pacific Ocean
Latitude and Temperature Range
Continental Shelf

Species	Adult Phase			Larval Phase		
	Latitude ° S.	Temp. ° C.	Occurrence	Latitude ° S.	Temp. ° C.	Occurrence
THYSANOPODA						
tricuspidata	15–16	26–21	Rare			
11° | 13° | 15° | 17°						
NYCTIPHANES						
australis	31–44	22–11	Common	34–44	21–12	Common
PSEUDEUPHAUSIA						
latifrons	15–32	28–16	Common	16–32	28–18	Common
EUPHAUSIA						
tenera	15–16	24–22	Rare			
recurva	28–39	24–15	Common	28–39	24–15	Common
similis	42–44	16–13	Rare			
lucens	43–44	13–11	Rare			
NEMATOSCELIS						
microps	16–34	23–16	Rare	28–30	23–17	Rare
difficilis	33–43	24–12	Common	33–43	24–12	Common
THYSANOESSA						
gregaria	30–43	23–12	Common	30–43	21–12	Common
STYLOCHEIRON						
abbreviatum	31–35	23–19	Rare			
carinatum	27–39	24–20	Rare			

To put the matter another way it is possible that a zooplankton association exists in cool sub-tropical ocean waters which may be regarded as characteristic of the area of formation of the water mass of the Western South Pacific central water (see Fig. 1, black squares), i.e., a cool sub-tropical association; and that this association at times extends northwards at least to latitude 34° S. This association includes such organisms as: the Euphausiids, *E. spinifera, E. similis, T. gregaria, N. difficilis;* and *Thysanopoda johnstoni;* Calanoid copepods typified by *Calanus finmarchicus;* Diacrid and Cavolinid Pteropods; Thaliaceid Tunicata such as *Iasis vagina;* and the Hyperiid Amphipod *Euthemisto australis.*

A further zooplankton association appears to be typical of the cooler tropical to warm sub-tropical conditions. It can be regarded as extending at least as far southwards as 34° S. latitude in its cycle of southern expansion; but in no case further south than latitude 38° S. The crustacean elements are fewer in numbers of individuals; and these are small, carrying little fat or oil, as compared with those of the cooler water association. Typical elements of this complex are the Euphausiids, *E. mutica, E. tenera, N. microps, Thysanopoda tricuspidata* and certain of the *"gibba"* group (but not *Euphausia gibba*); the Oxycephalid Hyperiid amphipods; the Tunicates, *Cyclosalpa pinnata, Ritteriella amboinensis,* and *Traudstedtia multitentaculata;* such Copepoda as *Nannocalanus minor, Euchaeta concinna,* and *E. marina*; and the Nudibranch, *Glaucus lineatus.*

Accompanying these two associations is an intermediate group of various species which apparently tolerate both sets of conditions with, however, a decided preference for the warmer. The Euphausiidae of this group include *E. gibba* and *E. recurva*; together with *N. difficilis* and *T. gregaria* as adults; other species of

this complex include the Pteropoda, *Creseis acicula* and *Creseis virgula conica;* the Chaetognath, *Sagitta hexaptera;* and possibly the Tunicates, *Salpa maxima* and *Thalia democratica.* This group rarely occurs further south than 39° S. but it may extend northwards to about 29° south latitude. It is interesting to note that *Euphausia recurva* is the dominating Euphausiid of the Western Australian slope waters (Eastern Southern Indian Ocean) between latitudes 25° S. to 35° S.)

TABLE 9.

EUPHAUSIACEA

Oceanic Distribution. Latitude 15° S. to 65° S.
Between Longitudes 145° E. and 155° E.
(South-West Pacific Ocean)
Latitude and Temperature Range

Species	Adult Phase			Larval Phase		
	Latitude ° S.	Temp. ° C.	Occurrence	Latitude ° S.	Temp. ° C.	Occurrence
THYSANOPODA						
tricuspidata	15–16	28–26	Rare			
monocantha	34–37	21–13	Rare	34	19–16	Rare
orientalis	15–34	28–20	Rare			
obtusifrons	34	21	Rare			
aequalis	34	17	Rare			
pectinata	34	17	Rare			
johnstoni	34–44	12–10	Rare	39	12–10	Rare
NYCTIPHANES						
australis	34–43	21–12	Rare	34–36	20–16	Rare
PSEUDEUPHAUSIA						
latifrons	16–32	28–18	Rare			
EUPHAUSIA						
sibogae	16	28	Rare			
pseudogibba	15–16	28–26	Rare			
diomedeae	16	26	Rare			
mutica	16–34	26–17	Rare			
tenera	16–34	24–20	Rare			
gibba	29–35	28–16	Common	29–34	21–17	Rare
recurva	16–39	26–15	Common	28–39	24–15	Common
spinifera	34–44	19–10	Common	34–45	19–10	Common
similis	34–54	17–7	Common	34–43	17–10	Common
lucens	41–50	14–8	Rare			
longirostris	43–53	11–5	Common			
vallentini	45–59	9–1	Common	50–54	6–4	Common
triacantha	54–61	5–1	Common	54–61	6–1	Common
frigida	56–65	2–(–1·5)	Common	50–58	1–(–1·3)	Common
superba	61–65	1·0–(–1·8)	Common	61–63	1·0–(–1·8)	Common
NEMATOSCELIS						
microps	16–34	23–16	Rare	15–34	28–14	Rare
difficilis	29–42	24–10	Common	32–42	23–12	Common
THYSANOESSA						
gregaria	24–43	23–12	Common	29–42	21–12	Common
vicina	47–63	(12–10)	Common			
macrura	55–65	(8–6)	Common			
NEMATOBRACHION						
flexipes	34–37	17–14	Rare			
STYLOCHEIRON						
affine	15–16	27–26	Rare			
suhmii	16–34	28–16	Rare	34–35	17–16	Rare
abbreviatum	16–34	28–14	Common	28–34	19–15	Common
longicorne	28–34	28–18	Rare	28	16	Rare
elongatum	33–34	28–18	Rare	34	20	Rare
carinatum	16–42	27–12	Common	24–42	24–12	Common
maximum	13	18	Rare			

The distribution of Euphausiid larval stages within the sector has been included in Table 9, together with their temperature range, in order to provide data for evaluating the discussion contained in Einarsson (1945), who considers that the "Zoogeographical grouping must be based on the thermopathy of the species in the reproductional area . . . ." In most cases the species were taken in too few numbers and too seldom for the comparison to be of value; but it is useful to note that several species which were very common in the

Eastern Australian area, with larval phases equally common, showed some reduction in the extent of the larval range. The most important of these species were as follows:

Euphausia gibba, in which the latitudinal range was about the same in the adults as in the larvae but in which the temperature range of the larvae was considerably less (adult, 28° C. to 16° C.; larvae, 21° C. to 17° C.).

Nematoscelis difficilis, in which both the latitudinal and temperature range of the larvae were narrower than those of the adults, together with *Stylocheiron abbreviatum* and *S. carinatum* which showed the same effect.

Nyctiphanes australis showed little temperature difference between adults and larvae in its shelf distribution (Table 8); but it is significant that, in spite of the large number of hauls made northwards of 34° S., the larvae of this very common species were not taken in that area, although adults were taken to 31° S., particularly during 1939.

In general the value of regarding the temperature range of the larvae as indicating the temperature range of the species lies in its application to areas where ocean currents may carry adults of a species far from their normal areas.

(f) CORRECTIONS TO OCEANOGRAPHICAL STATION LISTS.

This is the first available publication in which to make an important correction to the "Oceanographical Station Lists, Hydrological and Planktological Observations by F.R.V. 'Warreen' in South-Eastern Australian Waters," 1939-49; 2, 1940-42, published by the Commonwealth Scientific and Industrial Research Organization, Australia; Melbourne, 1951. In that publication a column has been entered, 1, under Planktological Observations, this is explained as, 1 = *Nyctiphanes* (Crustacea, Euphausiacea). The term *Nyctiphanes* is not applicable and the entry refers to adult specimens of species of the Euphausiacea in general. Larvae are not included. In addition, it must be noted that the plankton volumes listed in V. 1 and V. 2 are settlement volumes; those listed in V. 3, 1951, "Hydrological and Planktological Observations by F.R.V. 'Warreen' in South-Western Australian Waters, 1947-1950," are displacement volumes and therefore the two sets of data are not comparable. A full discussion of this subject is contained in Sheard (1947).

(g) LAYERING AND VERTICAL MOVEMENTS OF THE EUPHAUSIACEA.

It was hoped that an analysis of the plankton records and field observations would give worthwhile information relative to layering and vertical movements of Euphausiid swarms on the lines suggested by Johnson (1948) and Moore (1950) in their discussions of the scattering layers shown on echo-sounder traces (bathygrams). Since the plankton programme could not be designed to include repetitive day and night hauls at each station insufficient direct evidence on the subject as a whole could be obtained. Inferences only could be drawn from the data that some degree of layering and swarming existed, that limited vertical migration of the various species occurred, and that this was particularly noticeable during mating periods. Detailed tests indicated, however, that *N. australis* maintained its greatest density in the region adjacent to the sea-bottom in the adult phase, except during the period October to March, with the larvae rather more scattered. The slope and ocean species, *E. recurva, E. spinifera, E. similis, N. difficilis* and *S. carinatum* maintained their greatest density in the daytime at 100-200 metres, certainly rising to at least 25 to 50 metres at night, in swarms. It was noticeable that individuals with ripe gonads were taken very frequently in the upper 25 metres either by day or night. *Thysanoessa gregaria* formed an exception in that its zone of maximum concentration appeared to lie in the upper 25 metres particularly in the southern part of its range. This species and *N. australis* were the only species which formed large "rafts" on the surface; *T. gregaria* in both the breeding and non-breeding phase, *N. australis* during the breeding phase. These occurrences were noted chiefly in the South Australian, Bass Strait, southern Victorian and northern Tasmanian waters. The "rafts" were often up to an acre in extent mainly during the period October to March. They were preyed upon by concentrations of the muttonbird *Puffinus tenuirostris* and various terns which were feeding from above, and by either the southern bluefin tuna, or the striped tuna, feeding from below.

F. Differentiation, Development and Growth in the Euphausiacea.

(Tables 10-16; Figs. 4-17.)

In this section "differentiation" is used in the sense of increase in complexity and organization; "development" in the sense of visible morphological differentiation (serving also as an index of the changes in the organizational fields of the organism); and "growth" in the sense of an increase in the spatial dimensions and weight. Differentiation and development are treated together in the first part; growth is considered in the second; and the three aspects are discussed together in the third part. The treatment is descriptive, since rigorous experimental data cannot be secured until research vessels are fitted with specific laboratories in which the delicate and detailed rearing and physiological work can be carried out. A large amount of descriptive data has been obtained, however, as a result of the examination of the plankton hauls of oceanographical expeditions by various workers, notably Rustad (1930, 1934), Fraser (1936), John (1936), Einarsson (1945), Bargmann (1937 and 1945), and Boden (1950-1951). A consideration of that work, together with the results of the present study, permits of some restatement of the position regarding theories of development and growth in the order.

1. DIFFERENTIATION AND DEVELOPMENT.

(a) HISTORICAL.

The history of this subject has been given by several authors in recent years, and any exhaustive discussion would be labouring the point. As is the case with both the taxonomy and distribution of the species of the order, the literature on development is scattered, so that it is worthwhile to give a chronological summary of the chief references with a brief indication of their subject matter.

(i) Descriptions of Larval Development.

Among recent papers the following contain descriptions of series of larval instars together with references to earlier descriptions.

Lebour, 1926b. Development of *Stylocheiron suhmii* and *S. abbreviatum.*

Frost, 1935. Development of *Nematoscelis megalops* and *Stylocheiron longicorne.*

Fraser, 1936. A detailed and classic study on the development of *Euphausia superba.*.

John, 1936. Detailed studies of the development of: *E. frigida, E. vallentini, E. triacantha, E. longirostris,* and *E. spinifera.*

Gurney, 1942. A comparative study of the morphology of developmental phases of various Euphausiacea as part of a general study of the development of the Decapod Crustacea.

Bargmann, 1945. An equally detailed study of the later development of *Euphausia superba.*

Einarsson, 1945. Detailed discussions of: *Thysanopoda acutifrons, Meganyctiphanes norvegica, Nyctiphanes couchii, Thysanoessa longicaudata, Th. inermis, Th. raschii.*

References cited to: *Thysanopoda microphthalma, Thp. aequalis; Euphausia krohnii, E. longirostris, E. spinifera, E. triacantha, E. frigida, E. vallentini, E. superba; Thysanoessa macrura, Th. vicina; Nematoscelis megalops; Stylocheiron carinatum;* and *Pseudeuphausia latifrons.*

Gurney, 1947. Developmental phases of: *Thysanopoda cristata, Thysanoessa gregaria, Nematoscelis microps,* and *Pseudeuphausia latifrons.*

Boden, 1950. Developmental phases of *Euphausia pacifica.*

Lebour, 1950. Development phases of *Euphausia brevis, Thysanopoda tricuspidata, Thp. aequalis, Thp. cristata, Thp. orientalis, Euphausia tenera, E. hemigibba, N. megalops, N. microps, N. tenella, Stylocheiron carinatum, S. abbreviatum,* and *S. maximum.*

Boden, 1951. Developmental phases of *Nyctiphanes simplex.*

(ii) Theories of Development.

Sars, 1885. Larval phases and terminology defined.

Brook and Hoyle, 1888; Pleopods appear successively as simple rudiments, becoming setose in the same order.

Lebour, 1926d. Introduces idea that different orders of pleopod development may be characteristic of different genera; numbers pleopod stages successively, as if they presented a continuous series; concedes that a jumping of stages may occur in development, i.e., introduces the idea of "dominance" of certain stages.

Macdonald, 1927a. Develops idea of dominant stages; assumes a shortening of larval existence through a reduction of instars (citing *Meganyctiphanes norvegica*).

Rustad, 1930. Is the first worker to consider the developing organism as a whole. The paper has been overlooked by most of the subsequent workers but it contains valuable accounts of the development of various appendages. He summarizes as follows: "Considering now the single species, the early part of the development is almost schematic with no room for individual variations of importance, whereas in the late stages the specimens may show great variations which may even in greater or less degree efface the schematic picture of the development.

"If we try to find an explanation of this, the nearest supposition is that the external factors (supply of nourishment, temperature, etc.) are the determining ones. We must suppose that the young stages are passed through under approximately equal conditions; the spawning of the species is evidently limited by rather narrow biophysical borders, and during that time, moreover, the individuals gather in crowded assemblies. The earliest stages (nauplii and metanauplii) evidently take no nourishment and as long as the younger stages still live crowded, the conditions must be characterized as rather uniform for all individuals. In later stages, however, power of locomotion is increased, and, partly owing to this, and partly owing to physical motions in the layers, where the larvae now live, the individuals spread over a much more extensive and variated area so that the single individuals may come under very different conditions of life."

Fraser, 1936. In this exhaustive account of the early development of *Euphausia superba,* Fraser demonstrates that certain furcilia instars, numerically predominate at certain stages, and which he terms "dominant

stages'' should be regarded as successive instars. He draws no distinction between Furcilia and Cyrtopia phases; and suggests that the dominant stages ''should be regarded as the actual stages of that part of the developmental history, and the other stages as 'variants'.'' Without stating the case in detail Fraser makes some distinction between growth and development, as can be seen from his sentence: ''The series of moults may, in fact, be regarded as a kind of 'grid' superposed on a course of actually continuous development.''

John, 1936. Records the larval development of a number of antarctic Euphausiids and in the main agrees with Fraser (1936). He reintroduces the term ''post-larval'' for the phase commencing ''where the three pairs of posterio-lateral spines of the telson become reduced by the disappearance of the middle pair.'' Both Fraser and John appear to regard the Euphausiacea as ''arthropods in which continuous development is giving way to metamorphosis.'' This view is discussed later in the present report.

Frost, 1935, 1939. Accepts a theory of ''dominant stages'' and draws particular attention to the lower number of variants in ''oceanic'' as against ''neritic'' species.

Sheard, 1942. In a brief review states: ''It is extremely likely that particular minor phases of development which may be passed through are as much expressions of the available food supply as of anything else.''

Gurney, 1942. Presents a detailed comparative review of the development of the Euphausiacea, adopting in the main the view of John, Fraser, and Frost.

Einarsson, 1945. Rigorously examines the development of a number of North Atlantic species, and discusses the life histories traced out by earlier workers. After critical examination he adopts the views of John (1936), Fraser (1936), and Frost (1939), in general. In a section on ''Variations in the size of the larval stages'' he concludes: ''To account for the phenomenon that the larvae are bigger at lower temperatures it seems necessary to assume that there exist different relations between the temperature, and on the one hand the rate of development and on the other the rate of growth.'' In discussing the difference in the number of variants as between ''oceanic'' and ''heritic'' species he states: ''we therefore think it necessary to seek the explanation in the varying natural conditions of coastal waters as contrasted with the more stable and uniform conditions of coastal waters.''

Gurney, 1947. Discusses previous work, and considers that the term ''cyrtopia'' should be retained.

(iii) The Use of the Word ''Dominant.''

It is unfortunate that this term has come into use to denote those furcilia instars which are the most frequent in various plankton samples. On the one hand it has invited undue speculation on genetic and evolutionary aspects of development in the furcilia phase. On the other, it has masked the inadequacy of plankton sampling. In the first case, for example, the speculation ''that in the Euphausiacea continuous development is giving way to more marked metamorphosis'' (John, 1936; Einarsson, 1945) is given an extra air of credence by the use of the word ''dominant'' with its genetical implications when discussing furcilia development. In the second case, the result is that instars most common in plankton samples tend to be regarded as modal classes; and by an inversion, as evidence of the adequacy of the collecting methods to sample the species in all its characteristics.

A case in point is the following finding of Fraser (1936, p. 35) which has been accepted by later workers.

> ''The less advanced dominant stage becomes in each species the more advanced by the provision of setae on the non-setose pleopods present in the earlier stage, and the addition of one or more pairs of non-setose pleopods. In other words, each pleopod appears first in the non-setose form, and is provided with setae at the following moult.''

The last sentence appears to be reasonably true; but as Macdonald (1927a) recorded observing early furcilia of *M. norvegica* in which some pleopods remained non-setose after moulting, considerable laboratory work is required on this point. As a working hypothesis, however, it may be taken that an instar with non-setose pleopods is followed by one with those pleopods setose, and that a first furcilia stage can be distinguished consisting of those instars bearing no setose pleopods.

The first sentence in the finding quoted is not the equivalent of the second, and is not necessarily true. There are some indications that it is incorrect.

For instance, in illustrating his point, Fraser cites the case of *M. norvegica,* stating, ''The first dominant stage, that having three pairs of non-setose pleopods, is followed by one having three pairs setose and two pairs non-setose.'' John (1936), and Einarsson (1945), carry this concept further and regard ''dominant stages as successive instars.'' A consideration of figures 4 and 11 of this report show that this is not true regarding *N. australis* and *E. recurva* repectively, the only species which have been studied with the larvae at the point of ecdysis. (See Section F 2.) In *N. australis,* a consideration of figure 4 shows that instars, such as 3S2N and 4S1N do not necessarily arise from instars 3N and 4N respectively, but are contributed to via various paths from all the ''N'' series of instars, excluding 5N. The position is somewhat similar with regard to *E. recurva* (fig. 11).

Part of this over-simplification of the earlier authors arises from the use of ''stage'' in two senses, i.e., for a set of instars with a common characteristic (in this case non-setose pleopods alone, versus some pleopods setose); and for the most common instar in such a set. Part, however, lies in the faulty assumption, induced by the use of ''dominant,'' that the furcilia instar of the second stage most commonly found in plankton samples is necessarily derived from the most common instar of the first stage.

2. LARVAL DEVELOPMENT OF SELECTED SPECIES.

(Tables 10-13; Figs. 4-11.)

(a) METHOD.

Single plankton hauls from the South-Eastern Australian area contained in some cases complete sets of development phases, apparently of a single species, and detailed matching showed that series of larvae of *N. australis* were common. The chief method of determination consisted of matching, within single hauls, larvae in which the form of the next instar was clearly defined under the old cuticle, with that cuticle loosened preparatory to ecdysis. The series was followed through until an instar clearly referable to the species was obtained. In the case of *N. australis* that process was a relatively simple one as the characteristic two-segmented endopod of the seventh thoracic limb was identifiable in the early post-larval instars. In addition the shape of the carapace was definitive in the furcilia phases. In all larval phases the *habitus* was that of *N. couchii* as figured and described by Lebour (1925), and of *N. simplex* Boden (1951).

Measurements were taken, using a low-power binocular microscope with one eye-piece fitted with a micrometer. The readings were recorded in micrometer units. Only individuals showing the form of the next instar were measured. The total length was measured from the front margin of the carapace to the rear of the telson (excluding the telsonic spines) along the mid-dorsal line; the carapace length was measured from the front margin to the rear margin of the carapace also along the mid-dorsal line. In the advanced larvae and adults the forward point of reference was the base of the rostrum.

(b) NOMENCLATURE.

(Table 10.)

The nomenclature of larval development used in this report and summarized in Table 10 is as follows:

Naupliar Phase. The period of initial cephalic development. No segmentation apparent. Eyes present as rudimentary elements in the last stage. Antennular, antennal and mandibular limbs variously developed. Locomotion, a function of the developed limbs.

Nauplius Stages. Morphologically separable divisions of the naupliar phase some of which are passed through in the egg. Two stages have been named as follows: *Pseudometanauplius,* a non-functioning late nauplius stage, covered by a thin cuticle. In some species, e.g. *N. couchii,* the organism is reputed to hatch from the egg in this stage. *Metanauplius:* The final nauplius stage characterized by the absence of a mandibular limb, and the presence of rudimentary eyes.

Calyptopis Phase. The period of initial thoracic and abdominal development. Organism divided into two sections: Cephalo-thorax, and abdomen. Cephalo-thoracic appendages in various but minor stages of development. No pleopods, but uropods developing. Eyes present as rudimentary structures, covered by the carapace. Abdomen becoming segmented in later stages. Locomotion a function of the developed limbs, and of the abdomen as a whole in the later stages.

Calyptopis Stage I (CI). Abdomen unsegmented.

Calyptopis Stage II (CII). Abdominal somites distinct. Telson not separated from somite 6.

Calyptopis Stage III (CIII). Telson separated. Uropods appear.

As far as is known calyptopis stages I to III represent successive instars in all species.

Furcilia Phase (see Tables 10 and 16). Compound eyes, mobile and projecting beyond the carapace. Thoracic limbs progressively developing. Pleopods developing and telson spines gradually becoming reduced. Photophores developing. At some point the antennae become differentiated. Locomotion: a function of the antennae and of the segmented abdomen and uropods at first; later, developing pleopods take over the function of the antennae. The phase terminates with all pleopods setose and functional, the terminal spines of the telson reduced to one, and the middle lateral spine absent. In place of the varied number of furcilia stages proposed by earlier authors I propose three only. The reasons are discussed in the closing section of this report.

The furcilia stages proposed in this report are as follows:

Furcilia Stage I (FI). Eyes developed and free of the carapace, pleopods absent or present as non-setose rudiments. Terminal telson spines generally seven, sometimes reduced in number, e.g. *Pseudeuphausia.* Lateral spines three in number, the central spine always present. It is probable that a given specimen does not pass through more than two instars in this stage, i.e. "OP," and an "N" instar out of the 6 possible. In most cases only one instar (an "N") occurs.

Furcilia Stage II (FII). Some, or all, pleopods setose. Terminal spines sometimes reduced in number, e.g. *Pseudeuphausia; Nematoscelis microps, Stylocheiron suhmii; Thysanopoda aequalis.* Lateral spines three in number, the central spine always present. The pair of long lateral spines are unaltered at the base. Fifteen instars from 1S to 5S7sp.A are possible in this stage. It is highly probable that any given specimen passes through a limited number only.

Furcilia Stage III (FIII). All pleopods setose and functional. The pair of long, lateral spines are altered at the base. The terminal spines are progressively reduced to one (the median spine), (in at least one species of *Thysanopoda,* e.g. *T. tricuspidata,* the spines remain but are reduced to denticles). The stage termi-

TABLE 10.

A CODE FOR THE IDENTIFICATION OF LARVAL INSTARS IN THE EUPHAUSIIDAE

Code	Instar	Stage	Phase
N	Instars earlier than Pseudometa-nauplius	Nauplius	Naupliar
PMN	Pseudometanauplius	Nauplius 5	Naupliar
MN	Metanauplius	Nauplius 6	Naupliar
CI	First Calyptopis	Calyptopis I	Calyptopis
CII	Second Calyptopis	Calyptopis II	Calyptopis
CIII	Third Calyptopis	Calyptopis III	Calyptopis
OP	The furcilia instar with no pleopods present	Furcilia I	Furcilia
1N	One pair of non-setose pleopods present	Furcilia I	Furcilia
2N	Two pairs of non-setose pleopods present	Furcilia I	Furcilia
3N	Three pairs of non-setose pleopods present	Furcilia I	Furcilia
4N	Four pairs of non-setose pleopods present	Furcilia I	Furcilia
5N	Five pairs of non-setose pleopods present	Furcilia I	Furcilia
1S	One pair of pleopods, setose only, are present	Furcilia II	Furcilia
1S1N	One pair of setose, one pair of non-setose pleopods	Furcilia II	Furcilia
1S2N	One pair of setose, two pairs of non-setose pleopods	Furcilia II	Furcilia
1S3N	One pair of setose, three pairs of non-setose pleopods	Furcilia II	Furcilia
1S4N	One pair of setose, four pairs of non-setose pleopods	Furcilia II	Furcilia
2S	Two pairs of pleopods, setose only, are present	Furcilia II	Furcilia
2S1N	Two pairs of setose, one pair non-setose pleopods	Furcilia II	Furcilia
2S2N	Two pairs of setose, two pairs non-setose pleopods	Furcilia II	Furcilia
2S3N	Two pairs of setose, three pairs non-setose pleopods	Furcilia II	Furcilia
3S	Three pairs of pleopods, setose only, are present	Furcilia II	Furcilia
3S1N	Three pairs of setose, one pair non-setose pleopods	Furcilia II	Furcilia
3S2N	Three pairs of setose, two pairs non-setose pleopods	Furcilia II	Furcilia
4S	Four pairs of pleopods, setose only, are present	Furcilia II	Furcilia
4S1N	Four pairs of setose, one pair non-setose pleopods	Furcilia II	Furcilia
5S7sp.A	Five pairs of setose pleopods present. There are seven terminal spines on the telson together with three pairs of post-lateral spines the outer of which is not broadened at the base	Furcilia II	Furcilia
5S7sp.B	As for 5S7sp.A, but with inner pair of post-lateral spines broadened at the base	Furcilia III	Furcilia
5S6sp.	Five setose pleopods, six terminal spines	Furcilia III	Furcilia
5S5sp.	Five setose pleopods, five terminal spines	Furcilia III	Furcilia
5S4sp.	Five setose pleopods, four terminal spines	Furcilia III	Furcilia
5S3sp.	Five setose pleopods, three terminal spines	Furcilia III	Furcilia
5S2sp.	Five setose pleopods, two terminal spines	Furcilia III	Furcilia
5S1sp.1P.L.	Five setose pleopods, one terminal spine with three posterior lateral spines	Furcilia III	Furcilia
5S1sp.1P.L.	Five setose pleopods, one terminal spine, two posterior lateral spines, i.e., the central posterior lateral spine not yet lost. This may include a number of instars	Post-larval stages	Post-larval
5S1sp.1P.L.	Adolescent instars, characterised by the development of secondary sex characters	Adolescent stages	Adolescent

nates with the end of the phase. Seven instars are possible; but again, it is highly probable that any given specimen passes through a limited number only.

Pleopod emergence. Various symbols have been used to express pleopod characteristics in the instars of the furcilia phase. Einarsson (1945) suggested a numerical system, but any system of sequential numbering carries with it some implication of a necessary serial emergence and is an invitation to speculation on the evolution of species based on premises highly likely to be false. Consequently I have adopted a descriptive system (Table 10) based on the following working assumptions:

1. Pleopod emergence commences in the anterior abdominal segments not in the posterior; e.g. if four non-setose pleopods are present in an instar these will occupy abdominal segments 1 to 4, not 5 to 2, and so on.

2. Pleopods appears as non-setose lobes before appearing as setose lobes.

3. Changes in the armature of the telson are secondary in importance to pleopod emergence.

The notation is as follows:

OP = Furcilia in Stage I, with the eyes free, but without pleopods.
N = Non-setose pleopods.
S = Setose pleopods.

Numerals before the code letter indicate the number of pleopods present with the above characteristics. Consequently the notation 3N indicates an instar in which non-setose pleopods are present on the first three abdominal segments while the notation 3S2N indicates an instar in which the first three abdominal segments bear setose pleopods, and the last two bear non-setose pleopods. The notation 7sp., 5sp., etc. is used to denote the various terminal spine numbers; likewise the notation 3PL, 2PL, 1PL, records the numbers of pairs of posterior-lateral spines. Following Fraser (1936) the letters A and B have been used to denote the unaltered and altered post-lateral spine respectively.

These notations are detailed in Table 10, and are used in the text, in Tables 11 to 16, and in Figs. 4 to 11 of this report. As can be seen from Table 11 and Fig. 4, for example, each notation represents a discrete instar.

Post-larval Phase. This phase is an intermediate one, consisting of part of the Cyrtopia phase of Sars (1895). The abdomen and its appendages are fully functional. The thoracic appendage including the gills progressively complete their differentiation; but growth is incomplete. The antennae have ceased to act as locomotory organs, this cessation generally occurring in the third Furcilia. The phase terminates when the secondary sexual characters commence to develop and includes the period from the end of the furcilia phase to the end of adolescent stage 1 of Bargmann (1945), i.e. in the female the ovaries are in the primitive condition, unlobed and saddle-shaped, with the oviducts developing; the thylecum (in such species as possess this organ) is represented only by a straight band across the sternum. In the male the testes are simple with a developing uncoiled vas deferens. The first pleopod is undifferentiated.

Adolescent Phase. This commences with the development of the thylecum and of the petasma and with the emergence of other secondary characters (e.g. the change in proportions of the antennal segments of *Nyctiphanes australis* in the male (see Fig. 12), and terminates with sexual maturity—the adult phase. Including the egg, seven developmental phases are thus recognized.

(c) IDENTIFICATION OF *NYCTIPHANES AUSTRALIS*, ETC.

Since the adult segmental proportions are defined by the end of the second furcilia stage in this species (see Figs. 16-17) it is a relatively simple, although laborious matter, to work backwards from a later instar which is identifiable as belonging to the species to earlier instars and thus recognize the constellation of small characters which make up the *habitus* of the early instars. The process was made easier in this case of this neritic species as it was possible to hold specimens through single ecdyses (when the time involved was not more than twenty-four hours) in suitable containers aboard fishing vessels, and thus demonstrate that larvae possessing well-defined structures under the old cuticle moult into an instar possessing those structures externally. This was so in the case of pleopod, and of uropod emergence; abdominal segmentation in the calyptopis phase; and in modifications involving the loss of telson spines in the third furcilia stage. Attempts to rear larvae through a complete furcilia instar were not successful.

The naupliar phase (pseudometanauplius stage, and metanauplius stage), and the first calyptopis stage were obtained beyond doubt by a fortunate chance when eggs in the ovisacs of several females taken from a haul made in October, 1944, from a small net fastened to the cross-bar of a Danish seine operating in 25 fathoms at Ulladulla, N.S.W., hatched in the collecting dish. Larvae hatched from 30 eggs as typical pseudometanauplii with the partially enclosing fine, cuticular sheath; 18 of these shed the outer cuticle within a few minutes; one, observed under a low-power binocular microscope, slightly increased in volume before movements of the posterior part of the larva split the fine skin. Most of the resulting metanauplii died but 4 moulted into the first calyptopis stage within 12 hours. These instars do not differ from those figured by Sars (1885), Lebour (for *N. couchii,* 1925), Dakin and Colefax (1940, *N. australis),* and Einarsson (1945, *N. couchii*).

The first calyptopis carries two barely separated small reddish pigment spots toward the end of the

abdomen, and in later stages (commencing with the second calyptopis) these persist as two well separated red pigmented spots on the telson.

The frontal margin of the somewhat heavily built, oval carapace is slightly indented in the second and third calyptopis. This margin becomes an expanded frontal plate in the furcilia and post-larval phases, with its front margin either straight or very lightly indented in its mid-line (cf. Boden [1951, fig. 4, F], *Nyctiphanes simplex*). The short rostrum develops in early adolescence. There is no dorsal spine or hood at any stage and the carapace is not serrate.

By processes similar to those detailed above the developmental series of other Euphausiid species of the area have been worked out in more or less detail. Very short diagnostic summaries of the furcilia phase are given below to aid chiefly in the identification of *Nyctiphanes* larvae, the most important in the economy of the neritic fisheries. References are given to figures which will assist identification.

Nyctiphanes australis (Sars 1885; Dakin and Colefax [1940], figs., and compare *N. simplex* in Boden [1951]).

Larvae heavily built (in contrast to *Thysanoessa,* and *Stylocheiron*); frontal plate never produced to a rostrum and not rounded. Two red pigment spots on telson as in *N. couchii* (see Einarsson, 1945, fig. 9). Eyes large, circular, the corneal pigment never divided. Differentiation of the antennae occurs in furcilia stage 3.

Nematoscelis difficilis. Larvae moderately heavily built always with the frontal plate possessing a more or less pointed rostrum. Always four reddish pigment spots arranged as if on the four corners of a square toward the anterior end of the telson. Very much as in *Nematoscelis megalops* as described by Frost (1935, pl. 12 and 13); but the eye is divided into two parts at an early stage and the development of the elongate leg is complete at the end of the furcilia phase. The four pigment spots and the divided eye and the pointed rostrum separate these larvae from *N. australis.*

Euphausia spinifera (see John, 1936, fig. 40). Large and heavily built larvae with the frontal margin of the carapace fringed with denticles to the end of the furcilia phase. A posterio-dorsal spine is present on the carapace also until the termination of this phase. The dorsal spine on the third segment of the abdomen commences to develop in the first furcilia stage. Eyes large with the cornea not divided. Dorsal organ prominent. The fringed carapace, and carapace spine separates these larvae from *N. australis.*

Euphausia recurva (compare *E. pacifica,* in Boden [1950]). Moderately slender larvae. The eye itself is not constricted but the corneal pigment is separated into two more darkly red patches, an upper and a lower. The rounded rostral plate is not serrate, there is no dorsal spine. A small dorsal organ is present. The larvae may be separated from those of *N. australis* at all stages by the possession of a rounded frontal plate and by the internal division of the corneal pigment. The rostrum commences to form at the end of the second furcilia stage.

Thysanoessa gregaria. Slender larvae. Frontal plate always long, triangular and pointed (cf. Gurney, 1947, and compare *T. inermis* in Einarsson [1945], fig. 12), eyes divided at close of furcilia phase, divisions dark and nearly equal. The short pointed carapace, and the divided eyes separate these larvae from *N. australis.*

Pseudeuphausia latifrons. Larvae moderately heavily built. Frontal plate always deeply emarginate in mid-line with prominent lateral projections. (This character is closely the same as in the adult and is apparent from the first furcilia stage.) The calyptopis phase closely resembles that of *N. australis* in build; but no pigment spots have been observed on the telson, and the rear margin of the carapace projects in a somewhat hood-like manner over the first abdominal segment. No specimens of this phase have been found within the geographical range of that of *N. australis.* (For Figs. see Tattersall, 1930, and Gurney, 1947.)

Stylocheiron spp. (Gurney, 1947), very slenderly built larvae. Carapace produced into a sharp rostrum at an early stage, eyes divided, with the upper part smaller than the lower as in the adult (cf. *Thysanoessa gregaria*).

Some assistance is given in the separation of the species by a consideration of their geographic and temperature distribution. This serves as a rough guide only, as little is known of the nature and extent of the fluctuations in the hydrological conditions of the area. The distributional data so far obtained is contained in Tables 7 to 9, and is summarized below, for some species.

Nyctiphanes australis. Very common from latitudes 34° S. to 44° S., very rarely northwards to latitude 32° S. None were found in temperatures greater than 22° C. Major temperature range 15° C. to 19° C. (See table 7.)

Pseudeuphausia latifrons. Common from latitude 32° S. northwards, very rare south of latitude 32° S. The larvae of this species were not found in waters cooler than 15° C.

Nematoscelis difficilis. Common, particularly in slope waters, and in the upper layers, between latitudes 33° S. and 43° S. (and also as post-larvae). Area of commonest occurrence 36° S. to 39° S. Temperature limits 24° C. to 12° C.

Thysanoessa gregaria. Fairly common from latitudes 30° S. to 43° S., particularly in slope waters in the upper levels. Centre of distribution 36° S. to 41° S. latitude. Temperature limits 21° C. to 12° C., probable most favoured temperature range 17° C. to 13° C.

The above are the only species whose larvae have been recorded on the eastern Australian coastal shelf from latitudes 16° S. to 44° S., as more than isolated occurrences, involving few specimens.

(d) THE LARVAL DEVELOPMENT OF *NYCTIPHANES AUSTRALIS*.

(Tables 10 to 15; Figs. 4-10)

(i) Instar Sequences.

Anticipating the argument of Section F, part 5 of this report, the problem of defining the instar sequences of this neritic species as a whole involved the examination of samples representative of the latitudinal range of its larvae extending from 34° S. to 44° S., and of their temperature range (12° C. to 21° C.). This temperature range did not occur at each degree of latitude and it was considered that about 400 hauls would reasonably sample the area with some spread over the year to allow for seasonal productivity. Actually 398 hauls were taken. There was, of course, no possibility of assessing the past environmental history of any of the larval swarms which were taken, while no one sample or group of samples could be taken as necessarily representative of either the relative number of instars, or of the instar sequences present. Consequently, since it was desired to study the development of the species under conditions as widely representative of its ecology as possible, it was necessary to analyze each sample. The majority of these were reasonably small, containing between one and three hundred larvae, but one swarm contained approximately 4,000 larvae showing active development and this was analyzed in full (Fig. 9).

In all 36,720 specimens showing the form of the next instar were recorded and measured, and Table 11 and Fig. 4 records the total numbers which were found of each instar, together with the range of the

Table 11.

DEVELOPMENT OF *NYCTIPHANES AUSTRALIS*.

Lengths in mm.

Phase.	Total length			Carapace length			Moulting to
	Instar	Min.	Max.	Min.	Max.	No.	
1. Egg	Egg	0·3	0·4				
2. Nauplius	Na	0·4	0·5	0·4	0·5	920	PMNa, MNa
Nauplius	PMNa	0·55	0·6	0·4	0·5	360	MNa
Nauplius	MNa	0·5	0·75	0·4	0·5	1140	CI
3. Calyptopis I	CI	0·8	1·4	0·6	0·7	3870	CII
Calyptopis II	CII	1·4	1·9	0·7	0·7	4370	CIII, Op
Calyptopis III	CIII	1·6	2·4	0·7	1·0	4360	Op, 1N, 2N, 3N, 4N, 5N
4. Furcilia I	Op	1·9	2·6	0·9	1·0	1080	4N, 5N
Furcilia I	1N	2·1	2·8	0·9	1·0	1080	1S1N, 1S2N, 1S3N, 1S4N
Furcilia I	2N	2·15	3·0	0·9	1·0	1310	2S, 2S1N, 2S2N, 2S3N
Furcilia I	3N	2·05	3·0	0·8	1·1	2070	3S, 3S1N, 3S2N
Furcilia I	4N	2·6	3·3	0·9	1·1	1210	4S, 4S1N
Furcilia I	5N	2·9	3·0	0·9	1·0	30	5S7sp.A, 5S7sp.B
Furcilia II	1S1N	2·75	2·9	1·0	1·1	450	2S2N, 2S3N
Furcilia II	1S2N	2·7	2·8	1·0	1·1	40	3S1N, 3S2N
Furcilia II	1S3N	2·9	3·05	1·0	1·1	420	4S1N
Furcilia II	1S4N	2·9	3·0	1·0	1·1	60	5S7sp.A
Furcilia II	2S	2·8	2·85	1·0	1·1	50	2S3N
Furcilia II	2S1N	2·9	3·2	1·0	1·1	460	3S2N
Furcilia II	2S2N	3·0	3·6	1·0	1·1	490	4S1N
Furcilia II	2S3N	3·0	3·5	1·0	1·1	320	5S7sp.A
Furcilia II	3S	3·0	3·05	1·0	1·1	20	3S2N
Furcilia II	3S1N	2·9	3·2	1·0	1·1	940	4S1N
Furcilia II	3S2N	3·0	3·6	1·0	1·3	930	5S7sp.A
Furcilia II	4S	3·4	3·45	1·0	1·1	50	4S1N
Furcilia II	4S1N	3·0	4·0	1·0	1·3	1330	5S7sp.A, 5S7sp.B, 5S·5sp.
Furcilia II	5S7sp.A	3·4	4·0	1·1	1·3	2950	5S7sp.A
Furcilia III	5S7sp.B	3·6	4·35	1·1	1·4	330	5sp., 3sp.
Furcilia III	5S5sp.	3·6	4·8	1·1	1·6	490	3sp., 1sp., 3P.L.
Furcilia III	5S3sp.	4·1	4·6	1·3	1·8	620	1sp,3P.L
Furcilia III	5S1sp.3P.L	4·3	6·0	1·3	1·9	1570	1sp.2P.L
5. Post-larva	1sp.2P.L	5·25	7·5	1·7	2·1	2380	♂ or ♀
6. Adolescent	♂	6·7	11·3	2·2	3·2		
Adolescent	♀	6·9	11·2	2·1	3·2		
7. Adult	♂	11·3	14·0	3·2	4·3		
Adult	♀	11·2	14·3	3·4	5·0		

total length of each. Dotted lines indicate the various developmental paths (see Section 2, a). The numbers are rounded to the nearest ten in each case. It will be noted that of the 24 furcilia instars, the following are comparatively rare: 5N, 1S2N, 1S4N, 2S, 3S, 4S. Instars represented by the formulae 5S6sp. and 5S2sp. (not shown) were present in very rare cases. Several specimens were quite aberrant, possessing setose pleopods on one side, and non-setose pleopods on the other.

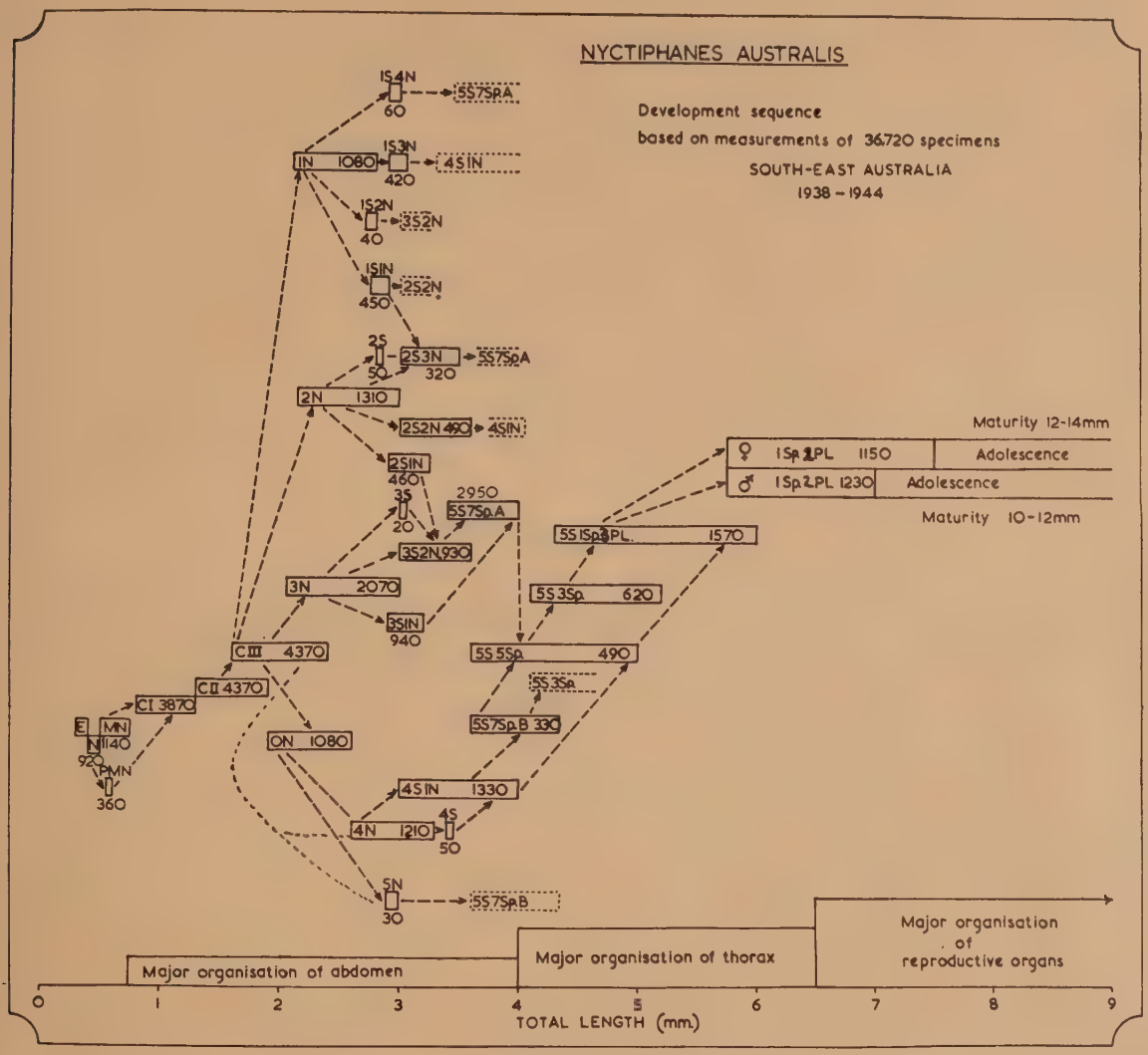


Fig. 4. *Nyctiphanes australis*, larval development, based on material from the full range of the species.

The instar recorded as 5S1sp. 3PL. has been named thus in conformity with Fraser's usage in *E. superba*, although by this instar *N. australis* the anterior pair of the three post-lateral telson spines has assumed the adult position on the telson, but the central, larval, spine is still present, while the posterior spine has not fully assumed its adult shape. In the post-larval instars the central spine has been lost; but the posterior spine is not yet fully shaped. The post-larval phase in general has been designated 1 sp.2PL. in table 11.

In Fig. 4, the instars recorded in Table 11 have been represented as rectangles with their base proportionate to the range of total lengths of the individuals found in each, the arrows linking successive instars.

Figs. 5 to 10 are inserted to indicate the developmental sequences which were obtained when small samples were analyzed from different parts of the range of the species. These demonstrate very clearly the possibility of obtaining misleading ideas regarding the "dominance" of instars in a species, when samples from one haul are analyzed, or when a mass sample is contributed to largely by a single swarm.

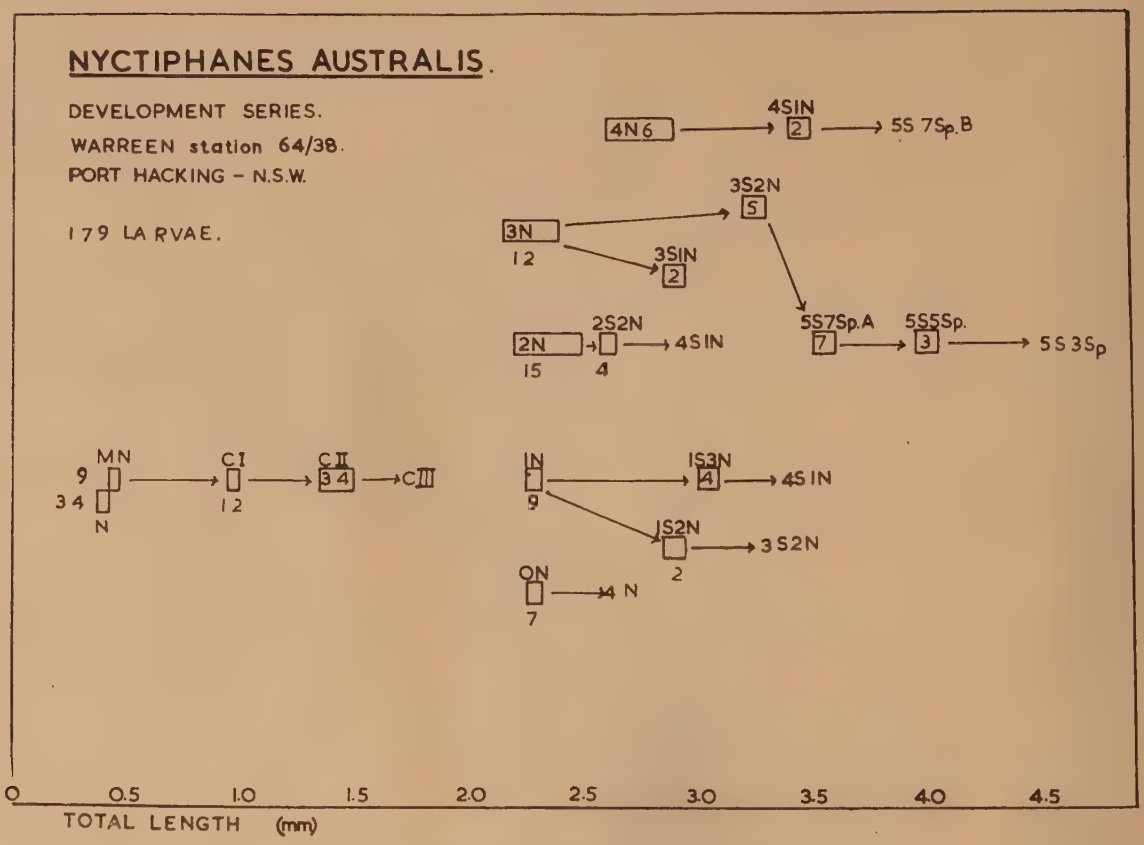


Fig. 5. *Nyctiphanes australis*, larval development.

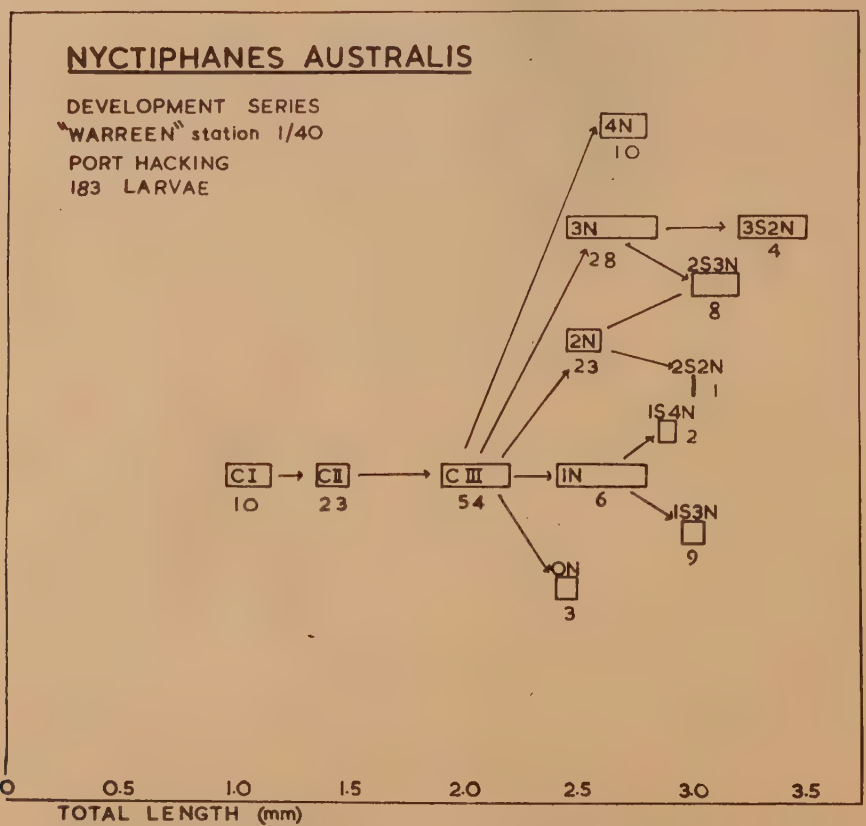


Fig. 6. *Nyctiphanes australis*, larval development.

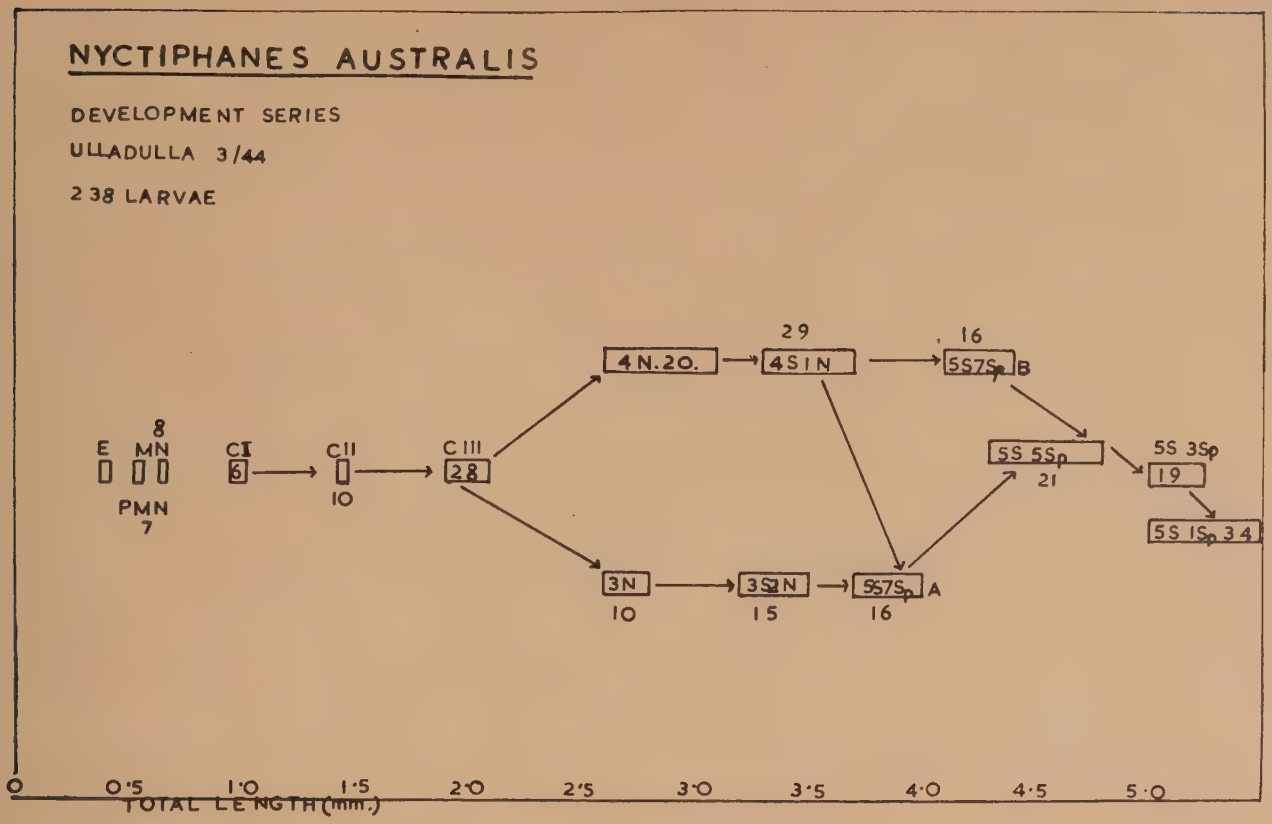


Fig. 7. *Nyctiphanes australis*, larval development.

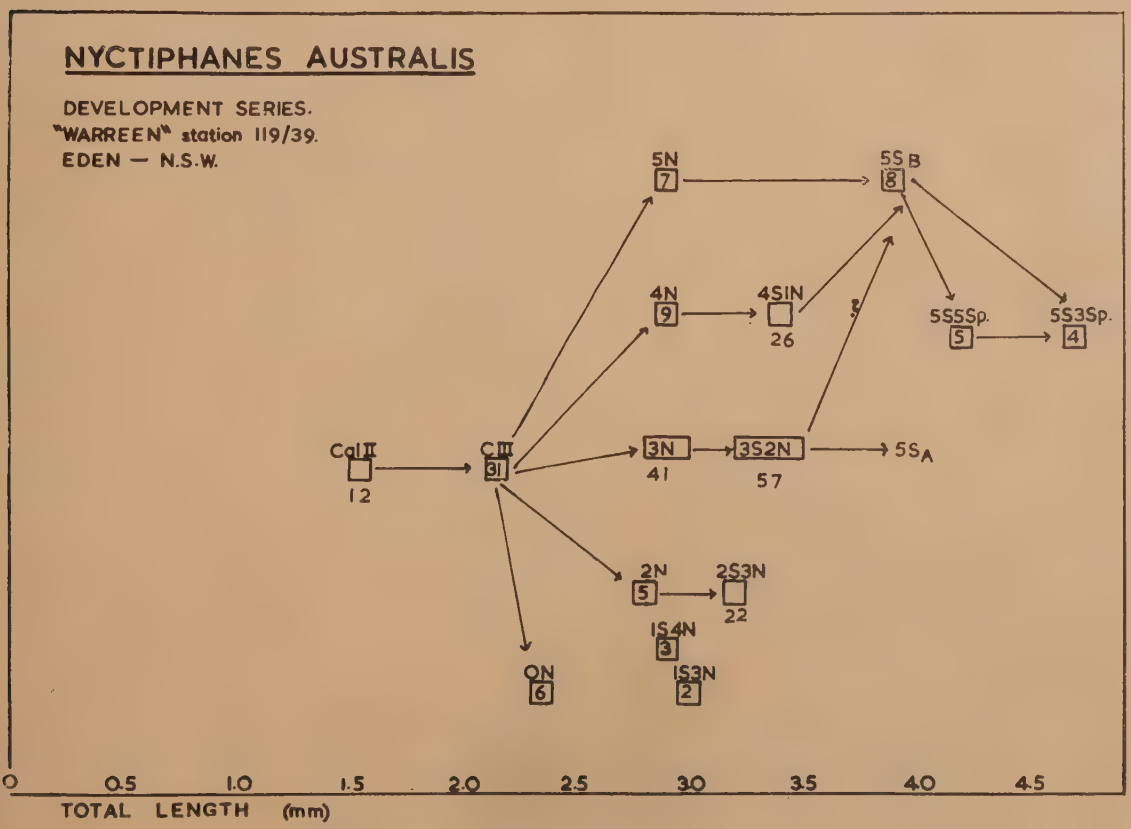


Fig. 8. *Nyctiphanes australis*, larval development.

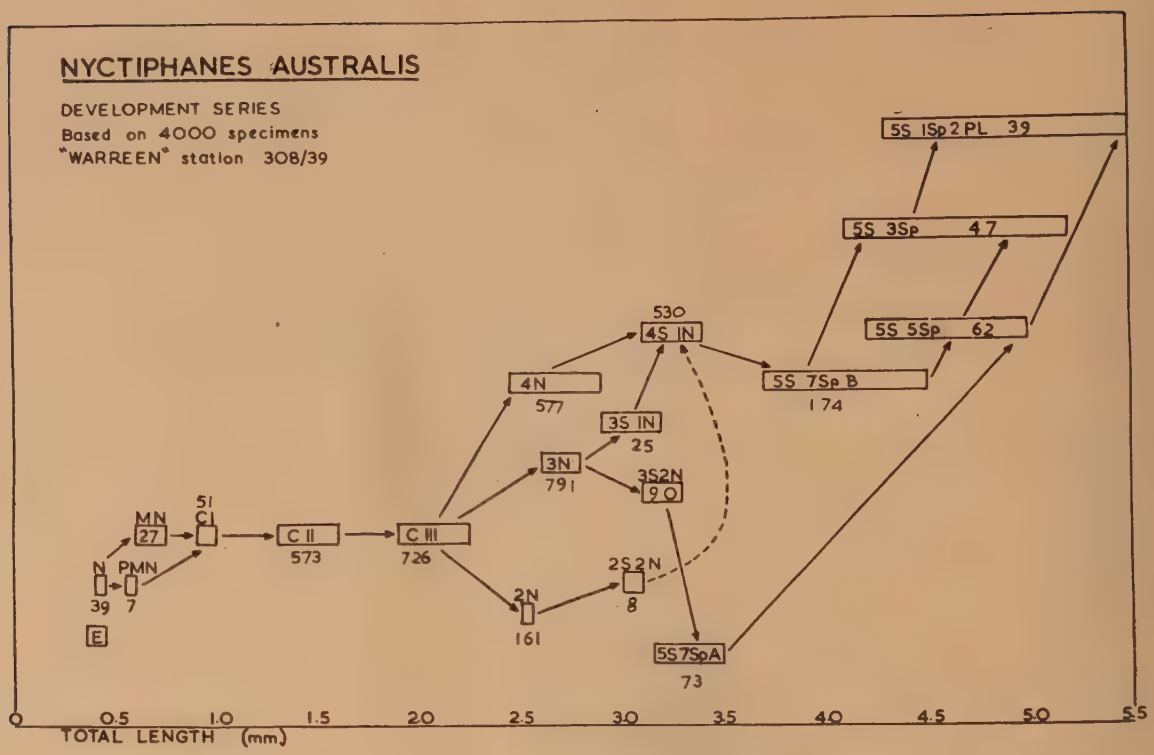


Fig. 9. *Nyctiphanes australis*, larval development.

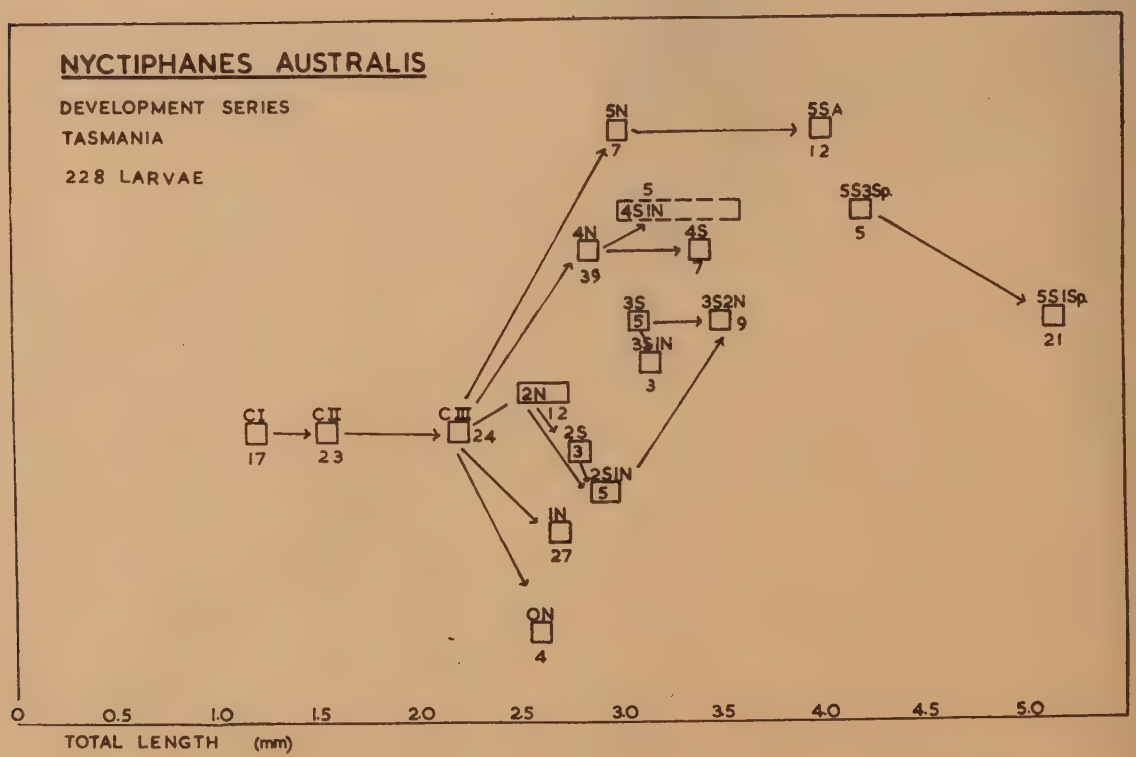


Fig. 10. *Nyctiphanes australis*, larval development.

TABLE 12.

NYCTIPHANES AUSTRALIS

Monthly occurrence of Larval Instars

Latitude 34° S. to Latitude 35° S.

South West Pacific Ocean, East Australian Coastal Shelf

1938-1944

Instars	January	February	March	April	May	June	July	August	September	October	November	December
MN	x						x	x	x	x	x	x
PMN	x						x	x	x	x	x	x
CI	x	x	x	x	x	x	x	x	x	x	x	x
CII	x	x	x	x	x	x	x	x	x	x	x	x
CIII	x	x	x	x	x	x	x	x	x	x	x	x
OP	x			x	x	x	x	x			x	x
1N	x					x	x				x	x
2N	x	x	x	x	x	x	x	x		x	x	x
3N	x	x	x	x	x	x	x	x	x	x	x	x
4N	x	x		x	x	x	x	x	x	x	x	x
5N												
1S	x											
1S1N											x	
1S2N											x	x
1S3N	x				x	x	x				x	x
1S4N				x								
2S											x	
2S1N											x	
2S2N	x										x	
2S3N	x										x	
3S											x	
3S1N	x	x									x	x
3S2N	x	x		x	x	x		x			x	x
4S											x	
4S1N	x	x		x	x	x	x	x	x	x	x	x
5S7sp.A	x	x		x			x	x				
5S7sp.B	x			x		x		x			x	x
5S5sp.	x			x	x			x	x	x	x	x
5S3sp.	x			x	x			x	x	x	x	x
5S1sp.2P.L	x	x	x	x	x	x	x	x	x	x	x	x
Adult	x	x	x	x	x	x	x	x	x	x	x	x
♀ ovig.	x	x	x	x	x			x	x	x	x	x
No. of Stages present	25	12	6	18	13	16	15	18	13	12	27	21
Hauls containing *Nyctiphanes*	18	5	2	3	1	4						
No. of hauls made	40	8	5	13	14	8	53	17	24	26	28	12

TABLE 13.

NYCTIPHANES AUSTRALIS

Monthly Occurrence of Larval Instars

Latitude 31° S. to Latitude 43° S.

(South-West Pacific Ocean, East Australian Coastal Shelf)

1938-1944

Stage	January	February	March	April	May	June	July	August	September	October	November	December
MN	x						x	x	x	x	x	x
PMN	x											
CI	x	x	x	x	x	x	x	x	x	x	x	x
CII	x	x	x	x	x	x	x	x	x	x	x	x
CIII	x	x	x	x	x	x	x	x	x	x	x	x
OP	x		x	x	x	x	x	x		x	x	x
1N	x		x			x	x			x	x	x
2N	x	x	x	x	x	x	x	x		x	x	x
3N	x	x	x	x	x	x	x	x	x	x	x	x
4N	x	x	x	x	x	x	x	x	x	x	x	x
5N					x				x			
1S	x											
1S1N											x	
1S2N										x	x	x
1S3N	x			x	x	x	x			x	x	x
1S4N	x	x	x	x	x	x		x				
2S											x	
2S1N										x	x	
2S2N	x			x		x				x	x	x
2S3N	x		x	x	x						x	
3S											x	
3S1N	x	x								x	x	x
3S2N	x	x	x	x	x	x		x	x	x	x	x
4S											x	
4S1N	x	x	x	x	x	x	x	x	x	x	x	x
5S7sp.A	x	x		x	x		x	x	x	x	x	x
5S7sp.B	x			x		x		x			x	x
5S5sp.	x			x	x			x	x	x	x	x
5S3sp.	x			x	x			x	x	x	x	x
5S1sp.2P.L.	x	x	x	x	x	x	x	x	x	x	x	x
Adult	x	x	x	x	x	x	x	x	x	x	x	x
♀ ovig.	x	x	x	x	x			x	x	x	x	x
No. of stages present	25	14	15	20	19	16	15	19	16	23	29	23
Hauls containing *Nyctiphanes*	30	7	3	10	8	6	11	13	17	28	29	22
No. of hauls made	90	22	9	31	28	22	55	31	31	66	55	40

(ii) Monthly Occurences of Larval Instars.

Table 12 records the monthly occurrences of larval instars during the period 1938 to 1944 on that part of the Eastern Australian shelf bordered by latitudes 34° S. and 35° S., while Table 13 gives this data for the areas bounded by latitude 34° S. to 43° S. Over the total range of the species breeding is continuous with this activity most intense in the warmer months from October to January. In these tables the results of a number of years are grouped in order to permit of some comparison of frequency of occurrence of the various instars, month by month. The numbers of hauls in each year were too few to permit of a comparison year by year, or month by month in each year, even in the most frequently worked area (34° S. to 35° S.); but other evidence indicated that there were considerable fluctuations in the numbers of *Nyctiphanes australis*, year by year. In addition it appeared likely that the range of the species, particularly in its larval phases, varied considerably in each year. This evidence included that afforded by the varying numbers of specimens, and of numbers of instars present in each haul; the numbers of individuals present in fish stomach contents; the varying presence of other, competing Euphausid species; and the presence or absence in some years and areas of fish species which are partly dependent on *Nyctiphanes australis*, e.g. the immature year groups of *Thunnus maccoyii*. No item was conclusive in itself; but the total presented a picture of variability which warrants intensive study in view of the importance of the species to the fisheries of the area.

(e) THE LARVAL DEVELOPMENT OF *EUPHAUSIA RECURVA*.

(Fig. 11.)

The majority of these larvae were taken at oceanic stations between latitudes 28° S. to 39° S. within a temperature range of 24° C. to 15° C. (see Tables 8 and 9) at depths of greater than 100 metres, although they were relatively common in some years, notably 1940 and 1941, in the deeper areas of the coastal shelf within the above latitudes. The greatest proportion of the specimens were post-larvae. Only 847 calyptopis and furcilia phase larvae were found which could be identified with certainty, and this number was distributed among 3 calyptopis and 14 furcilia instars (Fig. 11). A consideration of the false picture of larval development and of "dominance" by using small numbers of larvae of *N. australis* (e.g., of that given by 2,504 individuals of that species in the furcilia phase, Fig. 9) suggests that no trustworthy pattern of development or valid determination of "dominant" instars can be obtained from the available material of *E. recurva*. The species is a small one, specimens with ripe gonads occurring at a length range lying between 12 mm. and 17 mm.

(f) LARVAE OF *EUPHAUSIA SIMILIS*.

Although late furcilia, post-larvae and adolescents of *E. similis* were fairly common, other furcilia instars were rare, and were obtained only between latitudes 39° S. and 43° S., in temperatures between 15° C. and 10° C. These instars, the size range in mm., and the numbers found were as follows:

Calyptopis Phase. C2; 1·7 to 1·8 (2): C3; 2·7 to 2·8 (4).

Furcilia Phase. OP; 2·5 (1): 1N; 3·2 to 3·4 (6): 3N; 3·3 (1): 1S3N; 3·9 (1): 4S1N; 3·5 (1): 5S7sp.; 3·0 to 4·0 (3): 5S5sp.; 4·0 to 5·2 (3): 5S3sp.; 5·0 (1): 5S1sp.3PL; 6 to 7 (250).

The specimens all possess the small, lateral, keel-like projections on the lateral portion of the tergum of the first abdominal somite, as figured by Tattersall (1924, pl. 1, fig. 1), and I agree with John (1936) that this specimen, ascribed with some hesitation by Tattersall to *E. longirostris*, is a 1N instar of *E. similis*. The shape of the frontal plate of the larvae of this species is closely similar to that figured by Tattersall (*loc. cit.*, pl. 1, fig. 1), and there is no lateral expansion of this plate even when the rostrum is developing in the later furcilia and post-larval instars. Specimens with ripe gonads were taken with a length range of 18 mm. to 26 mm.

It was hoped to be able to secure specimens of *E. similis* var. *armata* in the early larval phases, but although considerable numbers of this puzzling variety were taken in the early post-larval instars, all showing strong keels on the third abdominal segment, no earlier instars could be identified with certainty.

(g) THE LARVAE OF *EUPHAUSIA SPINIFERA*.

As was the case with *E. similis*, late furcilia and post-larval instars of this species were fairly common over the range of the species (particularly in 1939); but earlier instars were restricted to south of 39° S. The following instars were noted:

Calyptopis Phase. CI; 1·4 to 1·9 mm. (4): CII; 2·2 to 3·0 (10): CIII; 3·0 to 3·8 (19).

Furcilia Phase. IN; 3·5 to 4·5 (22): 3N; 5 to 5·3 (3): 1S3N; 5 to 5·2 (11): 4S1N; 5·5 to 6·0 (3): 5S7sp.; B, 6 to 7·2 (9): 5S5sp.; 6 to 7·8 (421): 5S3sp.; 7·5 to 8·0 (7): 1sp.3PL; 8·5 to 9·0 (9).

Post-larval instars covered a size range of 9·5 to 11·2 mm. Specimens were obtained, with ripe gonads, over a size range of 23·5 to 30·0 mm. The only instars obtained not recorded by John (1936) were CI and 3N.

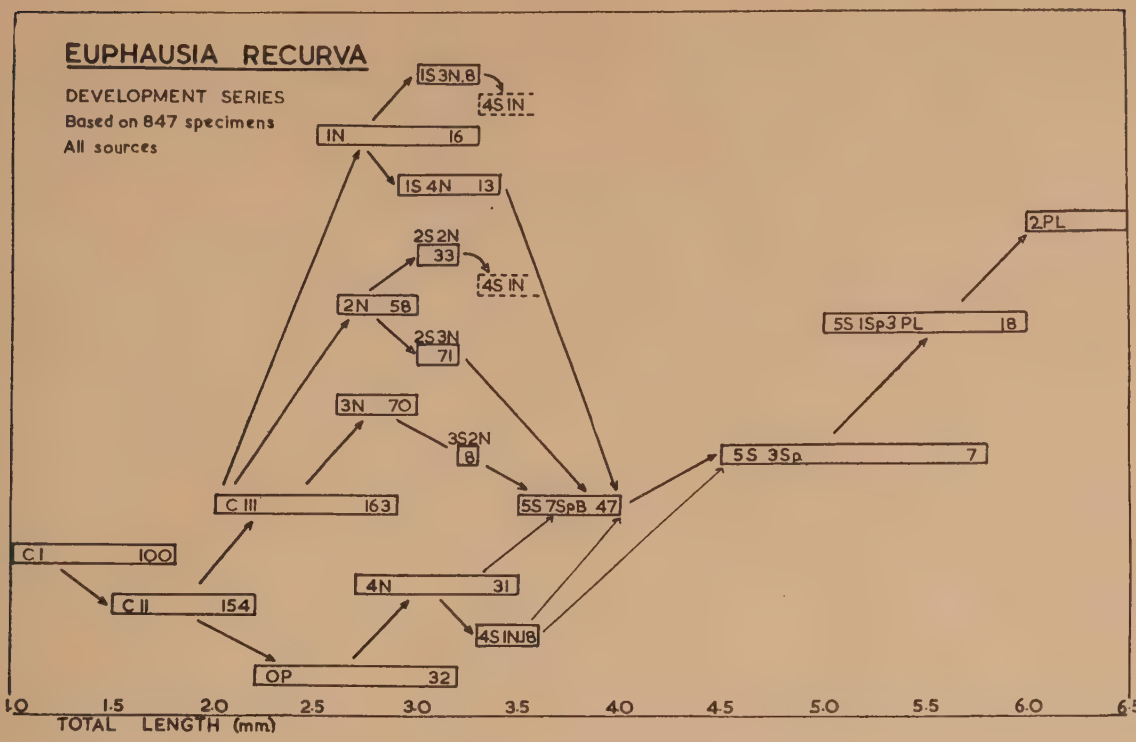


Fig. 11. *Euphausia recurva*, larval development.

(h) THE LARVAE OF *PSEUDEUPHAUSIA LATIFRONS*.

The records of the larvae of this species obtained by Tattersall (1936), Gurney (1947) from the Great Barrier Reef, and myself from Lat. 26° S. to 28° S. are given in tabular form for comparison.

Average sizes in mm. are given, and numbers, in the case of Gurney and myself.

Instar	*Tattersall*	*Gurney*	*Sheard*
CI			1·2–1·4 (6)
CII			1·8–2·0 (23)
CIII			2·0–2·5 (22)
OP	2·0	2·0 (17)	2·6–2·8 (16)
1N	2·2	2·3 (14)	2·6–3·0 (8)
2N	2·4	2·4 (5)	2·7–2·9 (7)
3N	2·4	2·6 (9)	2·8–3·1 (7)
1S1N	present	2·5 (2)	
1S3N	2·5	2·7 (2)	4·0–4·5 (7)
2S1N	present	2·5 (7)	
2S2N	2·6	2·7 (3)	
3S1N	2·8	2·8 (2)	
3S2N			
4S1N	3·0	3·5 (2)	4·0–4·6 (12)
5S7sp.A			
5S5sp.			Range 5·0–5·5 (8)
5S3sp.			
5S1sp.	3·4		Range 5·0–6·0 (23)

Specimens, with ripe gonads, were obtained at both areas over a size range, 10 to 12 mm.

(i) THE LARVAE OF *THYSANOESSA GREGARIA*.

The records of the larvae of this species obtained by Einarsson in the North Atlantic (Einarsson 1945), Gurney off Bermuda, Gurney (1947), and myself, along the Eastern Australian coastline in slope waters, are

given in tabular form. No size range is available for Einarsson's material and no numbers are given by Gurney.

Instar	*Einarsson*	*Gurney*	*Sheard*
MN			·9–1·1 (10)
CI			·9–1·4 (13)
CII			1·4–1·6 (14)
CIII			2·0–2·5 (12)
OP	(17)	2·4	2·3–2·8 (7)
1N			2·8–2·9 (2)
3N			3·0–3·5 (4)
5N	(27)	2·8–3·9	2·6–3·2 (26)
1S4N			3·3–3·4 (7)
2S3N			3·0 (1)
4S			3·3 (1)
5S7sp.A	(5)	2·7–3·2	3·0–3·7 (13)
5S7sp.B			3·4–3·6 (2)
5S6sp.			3·8 (1)
5S5sp.		3·1–3·5	3·0–3·8 (15)
5S4sp.			3·0 (1)
5S2sp.		3·25–3·9	
5S1sp.3PL		3·25–3·9	4·3–5·3 (11)
5S1sp.2PL		3·8–4·25	3·5–5·5 (9)
5S1sp.1PL		4·5–5·7	5·0–6·5 (30)
		Mature, 14 mm.	Mature, 11–14 mm.

My specimens conformed very well with those figured by Gurney (1947, figs. 5 and 6) and the petasma commenced to develop with the commencement of the 1PL instars at a length of about 5 mm., at which length developing gonads were present.

(j) THE LARVAE OF *NEMATOSCELIS DIFFICILIS*.

The early larvae of this species were taken generally in hauls below 50 metres although the later stages were fairly common at all depths. Those recorded below were taken from one swarm sampled in October, 1939, off Port Hacking in a night station, on the surface.

Calyptopis Phase. CI; 1·6 mm. (1): CII; 1·8 to 1·9 (3): CIII; 2·0 to 2·2 (3).

Furcilia Phase. OP; 2·4 to 2·5 (4): 1N; 3·1 to 3·3 (2): 2N; 2·6 to 3·1 (7): 5N; 2·8 to 3·5 (10): 2S3N; 3·9 (1): 3S2N; 3·4 (1): 4S1N; 3·8 (1): 5S7sp.A; 2·8 to 4·0 (9): 5S7sp.B; 4·5 to 5·0 (10): 5S3sp.3PL; 3·0 to 4·4 (10): 5S1sp.3PL; 3·8 to 5·5 (21): 5S1sp.2PL; 4·8 to 6·5 (13). (At the larger sizes of this instar the elongate limb was well developed.)

The size range of specimens with ripe gonads was 20 to 26 mm. Eggs from the ovisacs of ovigerous females ranged from 0·4 to 0·5 mm. in diameter.

The above sample was typical of the majority of the larvae which were examined (about 500 specimens). Additional instars found in other hauls were as follows: 3N; 2·8 to 3·0 (6): 4N; 2·9 to 3·1 (5): and 1S4N; 3·6 to 3·9 (5).

3. GROWTH, RELATIVE GROWTH, AND CHANGE OF FORM.

(Tables 14 and 15 (see appendix), Figs. 12 to 17.)

(a) HISTORICAL.

Although length measurements of various stages in the life history of the Euphausiacea have been recorded by a number of authors, Ruud (1932) was the first to endeavour to relate length and time, thus obtaining an approximate time required for the development of a species to maturity (in his case *E. superba*). The essentials of his method were to divide the adolescent and mature specimens into their respective groups; to measure the lengths of a number of specimens in each group in the monthly catch; and to plot the monthly averages on a time line. The curve so obtained was combined with one derived from a similar treatment of larval stages. As a result he decided that *Euphausia superba* required two years in which to reach sexual maturity.

John (1936), with a larger amount of material, spread over a longer time range, and with much more detailed information on the biology of the species, used approximately the same method and arrived at the same conclusion regarding the time to maturity. He considered, in addition, that the larvae of *E. superba* reached a length of about 10 mm. by the end of their first summer, that a length of over 24 mm. was reached at the end of the first 12 or 14 months; and that, with advancing development, a lengthening time was spent in a particular stage.

Again using the same method, Einarsson (1945) grouped his material and worked out approximate ages of a number of species from the North Atlantic. These may be listed as follows:

Those maturing at the end of the second year: *Thysanopoda acutifrons* (length 35 mm.); *Thysanoessa inermis* (length about 22 mm.); *Thysanoessa raschii* (length about 22 mm.).

Those maturing at the end of the first year: *Meganyctiphanes norvegica* (length about 27 mm.); *Thysanoessa longicaudata* (length about 11 mm.).

He considers that there is a close correlation between temperature and the maturing of the species both in respect to time and size, i.e., the lower the average temperature the longer the time and the larger the size. He concludes that below certain minimum temperatures development and the process of maturing cannot take place in the same area, "but as the spawning season (outside of which the maturing stimulus appears to be absent) is strictly limited, the animals live through a second growth season in which they become larger than animals developing and maturing in one year."

Bargmann (1945), in an intensive study of adolescent and mature phases of *E. superba,* refined the method considerably by dividing the adolescent and adult phases into stages, based on the degree of maturity of the gonads, and of the petasma and thylecum. She demonstrated a slower growth rate in the female than in the male, and considers that "the main factor which influences the growth rate of *E. superba* is food."

Each author derives a growth curve for the species under discussion; but Bargmann endeavours to allow for the heterogeneity of the material by giving "a diagrammatic representation of the generations arising from three batches of eggs spawned in February, March and April" (Bargmann, 1945, fig. 10). This in effect gives confidence limits to the growth curve obtained from mass samples and thus a better representation of the process of growth.

Even with this refinement the method is crude and the results inexact; but in the present state of knowledge no other is available. Crustacean biometrics are in the same state as were teleost biometrics before the discovery of the significance for age-grouping of certain of the "rings" on scales and otoliths in giving some check on the adequacy of length-frequency data. The "Reproductive Stages" of Ruud (1932) and Bargmann (1945) are the nearest approach to this type of cross reference, so far found in the crustacea; but they appear to be most useful in areas and species where the spawning season is relatively short. The method, however refined, rests on two assumptions, the first that each of the sets of populations present in each month is sampled, and the second that this sampling is random. In view of the inadequacy of all types of plankton nets with respect to Euphausiids, and of the swarming characteristics of various phases, together with their very different diurnal migratory rhythms, it is unlikely that the assumptions apply.

During the present investigation analysis was made of the extensive material of *Nyctiphanes australis* on the above lines, and this indicated that possibly a year was required for the maturity of the species, but, in view of the above factors, together with the long spawning period of from eight to eleven months (Tables 12 and 13) the estimate is little more than speculation.

(b) RELATIVE GROWTH IN *NYCTIPHANES AUSTRALIS.*

(Figs. 12 to 14; Tables 14 and 15.)

No investigations into the relative growth of parts of individuals of a Euphausiid species have been made hitherto; and studies of change of form have been by means of series of drawings showing changes of shape of the whole or of parts during larval instars (e.g., those of Fraser [1936], John [1936], etc.). In addition Fraser (1936) has provided detailed series of length measurements of various appendages from which approximate curves of relative growth could be obtained. Unfortunately the only length measurement he recorded of a major part of the organism was the total length. This is not a particularly useful referent for relative growth purposes unless the part under comparison is a discrete portion of the whole, as would be the case with the carapace, or the abdomen, or of segments of the abdomen. In the case of the thoracic appendages measured by Fraser, which are functional elements of the thorax, the referent should be the carapace length, as there is a substantial degree of correlation between the proportionality of parts and the absolute size of the related major portion of the organism. In any case the data are not of a high order of reliability for the derivation of allometric equations since both biologic and chronologic time are unknown variables. The same objection holds with regard to the data relating to *Nyctiphanes australis* presented in Table 15 and Figs. 12 to 17. The material used for this brief study was obtained from a net-haul made in the region of Ulladulla, New South Wales, during a plankton net reliability test denoted as Ulladulla 3/44. (The developmental data of Fig. 7 were obtained from a later net-haul of the same series.) The swarm which was measured consisted of developmental phases ranging from a nauplius obtained from an egg from the ovisac of a female *N. australis* to probable second maturity males and females. Although present as a single swarm, the individuals were thus representative of an unknown number of environmental influences. The sample conforms in these respects to the type D data of Richards and Kavanagh (in Clark and Medawar, 1945), in which age variation and that due to individual differences are intermingled inextricably. To some extent biologic time sequences may be erected on a basis of development sequences on the assumption that the successive biologic stages in a heterogeneous sample represent successive chronological stages. In view of the unknown effects of temperature in itself, and of that of nutrient intake at different temperatures, this assumption is of little value. A further assumption

implicit in the statistical analysis of this type of material is that the length frequencies are distributed normally about the mean. In actual fact such distributions are highly skewed in *N. australis*, just as Pearl and Clawson (1907) found for frequency distributions of segments of *Cambarus propinquus*. It is true that suitable transformations may be found, logarithmic or otherwise, but these obscure the original data, and the equations and curves so obtained yield little information of biological value. For this reason no attempt has been made to fit equations to the data given here, but the graphs have been presented in order to demonstrate possible growth characteristics of various parts of the organism at different development phases.

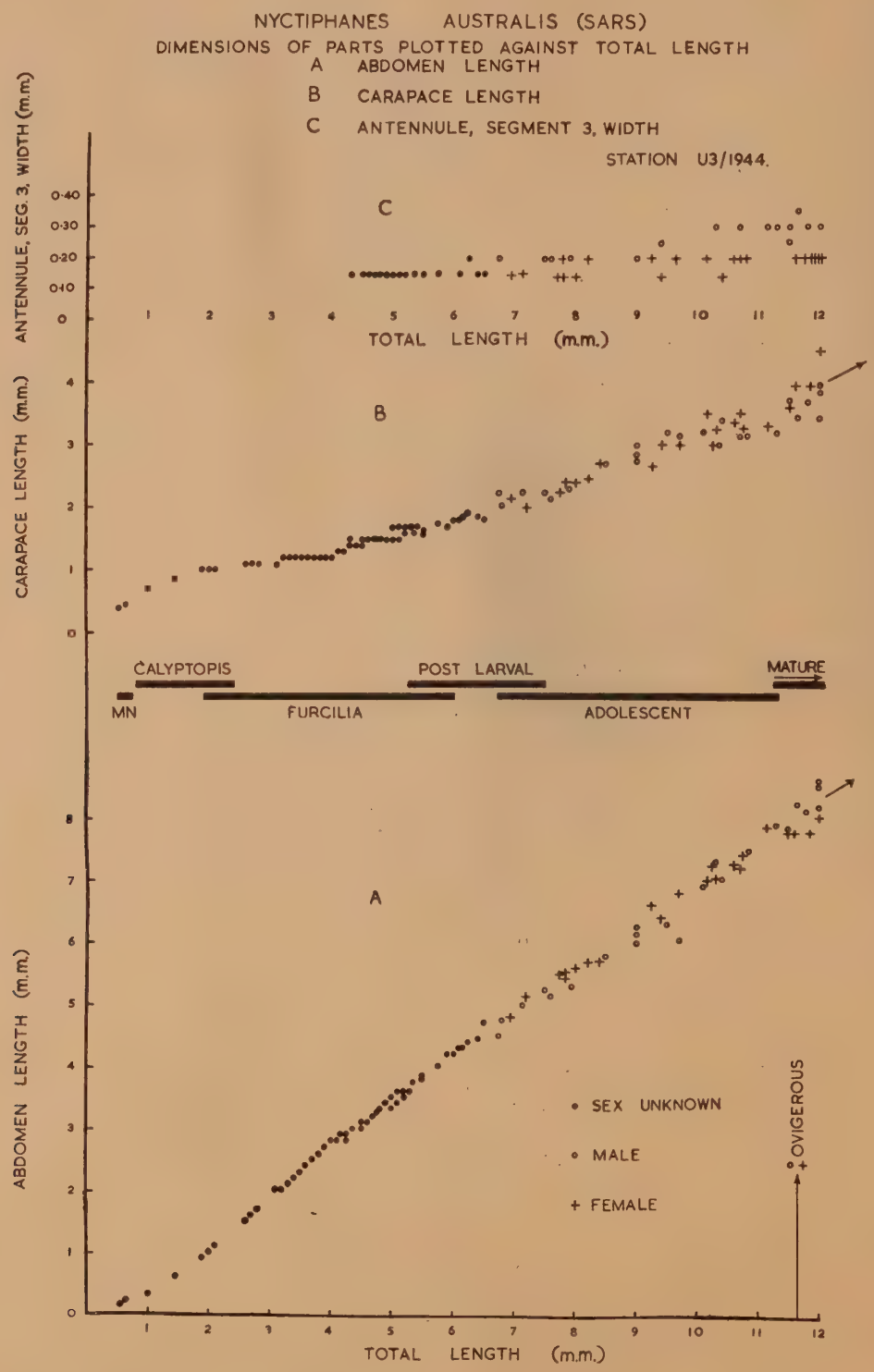


Fig. 12. *Nyctiphanes australis*, relative growth and developmental phases.

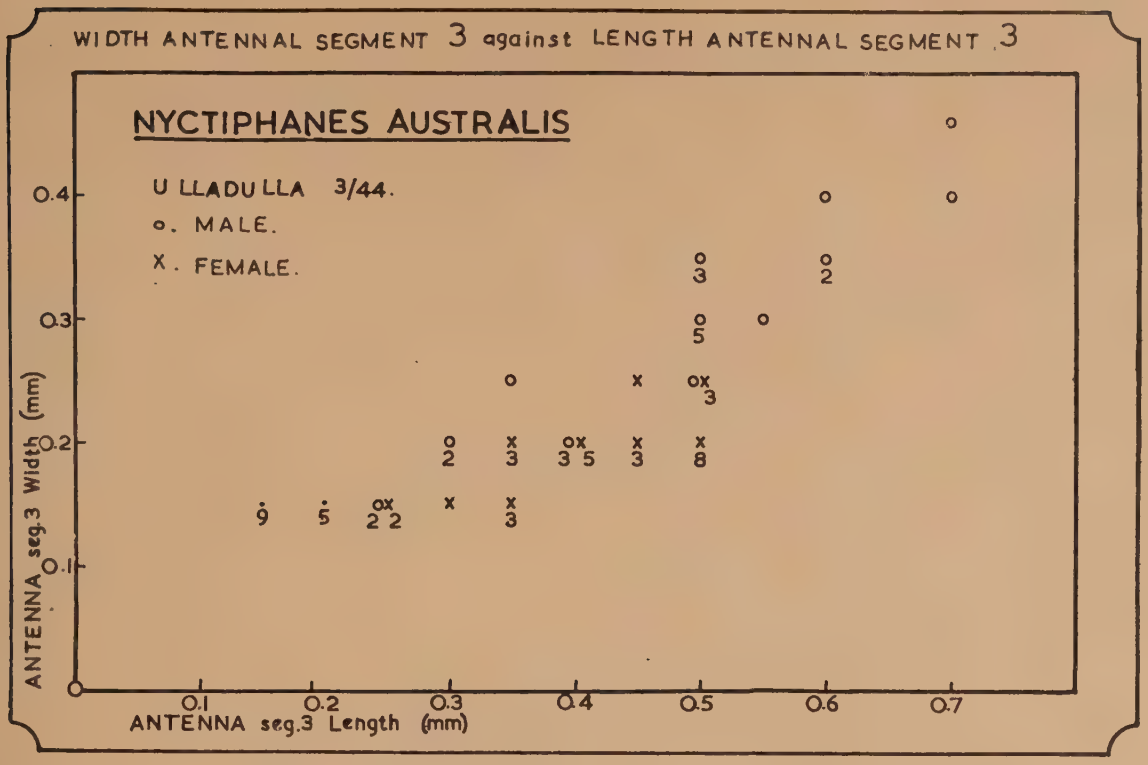


Fig. 13. *Nyctiphanes australis,* regression of width against length of antennular segment 3.

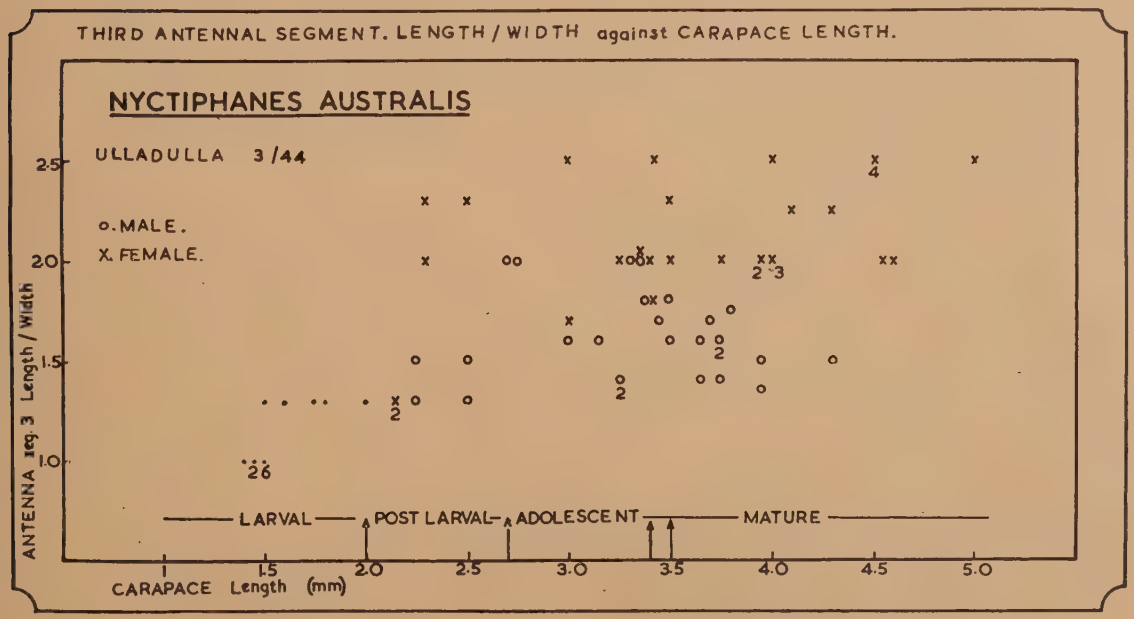


Fig. 14. *Nyctiphanes australis,* relative growth of antennal segments 3; and developmental phases.

Figure 12 records the growth of abdomen and carapace (expressed as length in the mid-dorsal line) plotted against the total length. The length range of the various phases, obtained from the previous analysis of all the samples of *Nyctiphanes australis* (Fig. 4), is given to act as indications of biological age. In this species there is a secondary sex difference expressed in the peduncle of the antennule, accordingly the width of segment three of the antennule is plotted against total length, and development phases in the same figure.

The form of the growth curve of the carapace (Fig. 12 B) i.e., a rapid increase in the early calyptopis stages; a retardation to the end of the second furcilia; and an increase at about the original rate from then on, with a slightly slower rate for males in the late adolescent and maturity phase: was duplicated (although with

slightly different growth rates) in a number of other samples. In the case of this species the retardation in carapace growth during the first two furcilia stages is accompanied by a retardation in the emergence and growth of the thoracic appendages. Development of the appendages of the cephalo-thorax is resumed in the later instars of the third furcilia. The most notable of the other changes which occur in that stage are the differentiation of the antennae, the rapid emergence and elaboration of the gills, and the progressive reduction of the larval telsonic spines.

The secondary sex variation characteristic of the antennules is illustrated in Figs. 12c, 13, and 14. As regards the third antennular segment, i.e., that in which the variation is most apparent, the width increases at a slower rate than the length in the female; but at a rate more nearly approximating to the rate of increase of length in the male (Fig. 13). The result is a cylinder about 2 to 2·5 times as long as wide in the mature female, and about 1·5 times as long in the mature male. The change in proportion is apparent in the early post-larval phase, before any differentiation of the petasma and thylecum occurs and while the gonads are yet in a very early stage of development. In second maturity males (not figured) the segment is contorted and sub-rectangular, departing very considerably from the simple cylinder of the female. The muscles contained in this segment in the male, even in early maturity, are bulkier than in a female at any stage of maturity, while the antennular flagellae appear to be more massive. In view of the plastic nature of the segments of crustacean appendages at ecdysis the difference in form of the segment may be rather a function of a bulkier, more complex muscle mass, than an expression of a directional growth in the ectodermal cell sheet which ultimately forms the chitinous sheath of the segment. Linear measurements are certainly not adequate to express the relationships involved. In this and in all other cases in literature (see Growth Bibliography) one is more inclined to regard the morphological data, based on linear (and for that matter wet weight) measurements as only partially reflecting the trends of relative growth changes, and as not susceptible to detailed analysis (see discussion in Needham 1942, pp. 551-562, and in Zuckerman *et al* 1950).

(c) CHANGE IN BODY PROPORTIONS IN *NYCTIPHANES AUSTRALIS*.

(Tables 14 and 15; Figs. 15 to 17.)

In shape, the body of *N. australis* (and of other species of the Euphausiacea) may be regarded as consisting of two half cylinders, joined in a straight line. The forward half cylinder, the cephalo-thorax, is slightly wider and deeper than the after cylinder, the abdomen, which is again divided into six half cylinders, roughly equivalent in dimensions. The abdomen terminates in a plate-like projection, the telson, rectangular in the larval phases, sub-triangular in the adult.

In order to obtain an indication of the relative proportions of the major body segments at each phase of development, the lengths, recorded as micro-units (1 unit = 0·017 mm.), were measured in the mid-dorsal line, using the clearly defined segment boundaries as markers. The lengths were converted to percentages and recorded in Table 15 as follows:

Line B: the divisor is the total length of the animal from the front of the carapace (excluding the rostral projection in the adult) to the rear margin of the telson (excluding the terminal spines).
Line C: the divisor is the abdomen length, including the telson.
Line D: the divisor is the abdomen length (segments 1 to 6).

Each specimen referred to in Table 15 was given a serial number, and certain biological characteristics of the individuals were entered against each serial number in Table 14. In this table the instar characteristics up to the end of the post-larval phase (specimen 66) were recorded using the code defined earlier in this report. In this species no thylecum exists of the form of that in *Euphausia superba*, while the petasma is of a very different form, so that the adolescent and adult stages worked out for that species by Bargmann (1945) could not be used.

In Fig. 15 the "x" axis represents the percentage segment length relative to total length for the segments, carapace, abdomen, and telson, respectively. The left-hand "y" axis provides a separating set of markers provided by the total length in each case, while the right-hand side of the "y" axis provides the development phase length range corresponding to these lengths, and thus gives an approximate measure of physiological time in the sense of Brody (1945, pp. 712-740).

It will be seen that the relative proportions of carapace and abdomen are fairly well stabilized by the end of the first furcilia stage, i.e., when all abdominal segments are equipped with non-setose pleopods, and that there is some suggestion that abdominal growth is commencing to slow down, relative to the carapace, at an early period in the third furcilia stage (cf. Fig. 12). The telson develops rapidly in the calyptopis and early furcilia stages, the rate declining thereafter. Functionally there is a gradual, not a sudden, transfer of the prime locomotive agents from the front to the rear section of the animal during the furcilia stages.

The growth partition relationships obtained from this data are, of course, empirical, and strictly speaking no extrapolation can be made from them. They are in accord, however, with the observations made while examining the many thousands of larvae contained in the "Warreen" plankton hauls, and the possibility is that this type of growth partition may be approximately characteristic of the species within the range of environmental conditions covered by the plankton tows.

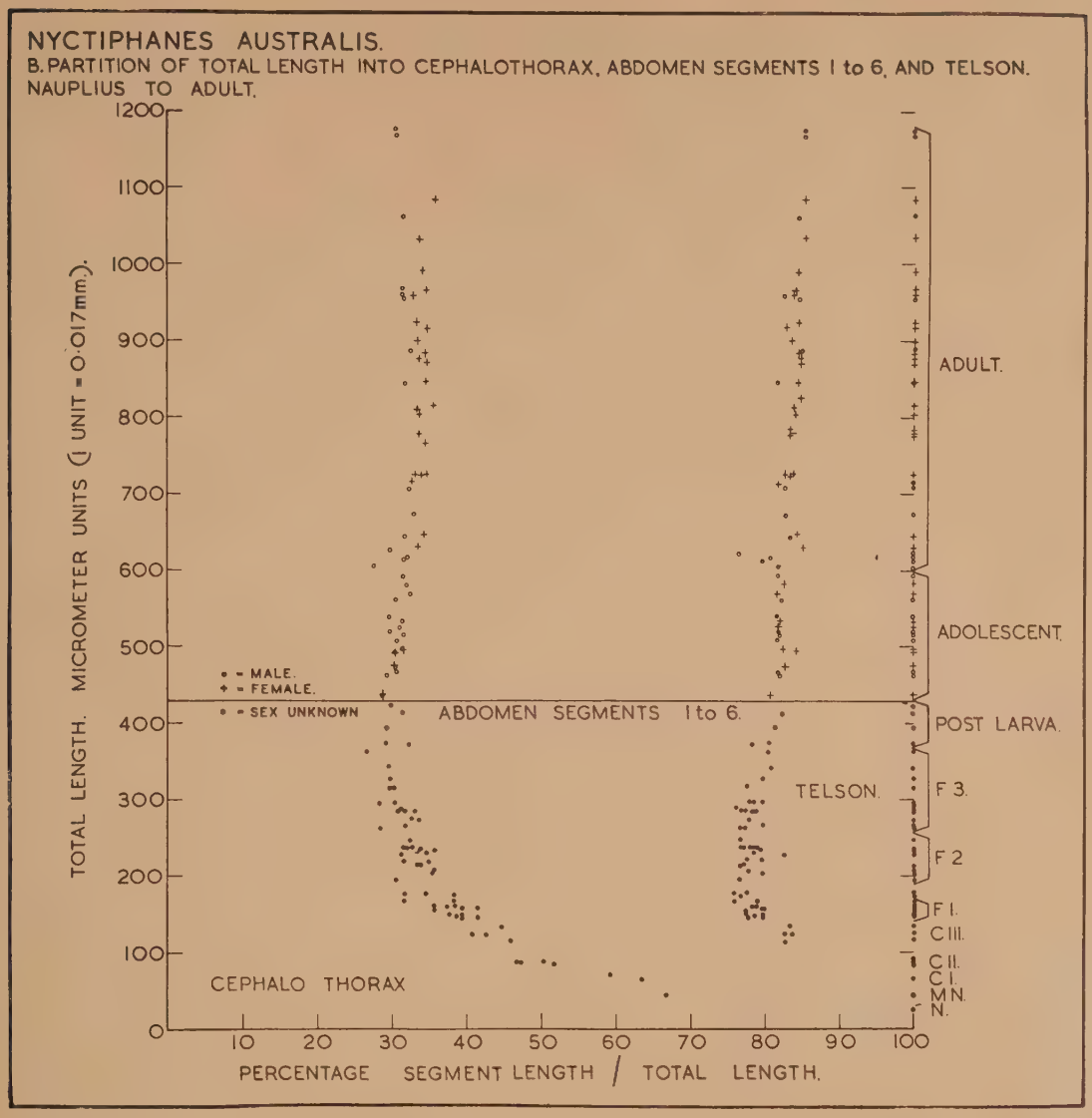


Fig. 15. *Nyctiphanes australis*, partition of total length; and developmental phases.

Figure 16 records the same type of data, in the same form for abdominal segments 1 to 6, and the telson respectively, with the marker axis the length of abdominal segments 1 to 6, together with the telson. The telson again shows a more rapid early development in respect to the abdomen as a whole, the period coinciding with the rapid emergence and development of the uropods (appendages of the sixth abdominal segment, which also develops rapidly at this period) during the late calyptopis and early furcilia stages.

In Figure 17 the partition of the abdomen proper into its respective segments is shown in the same manner as in the foregoing figures. This section of the animal is a functional whole with each segment contributing more or less equally to the function of locomotion, partly by pleopod movement, and partly by abdominal flexure which drives the efficient caudal fan consisting of the uropods and telson. In such a system it could be expected that there would be a tendency to an equality of proportion of the segments and that this would be approximated when the respective appendages became functional. By the close of the stage which I have nominated as furcilia 2, the pleopods are functional with their respective muscle systems well developed, the condition of comparative equality in segment proportions (expressed as length) has been attained, and the period of rapid growth of the segments is virtually over.

Combining the results shown in Figures 15 to 17 they make a case for a closer integration of function and form than hitherto in the study of the development of the Euphausiacea, where the prime insistence has been on morphology, with function, when it has been considered, regarded as occurring suddenly rather than gradually emerging. (In passing it is legitimate to ask on this basis whether the relative sterility of the various mathematical analyses of growth, relative growth, and form, is not due to a like divorcement of function and form. In this respect the essay of Waddington in Zuckerman *et al* (1950) is very much to the point.)

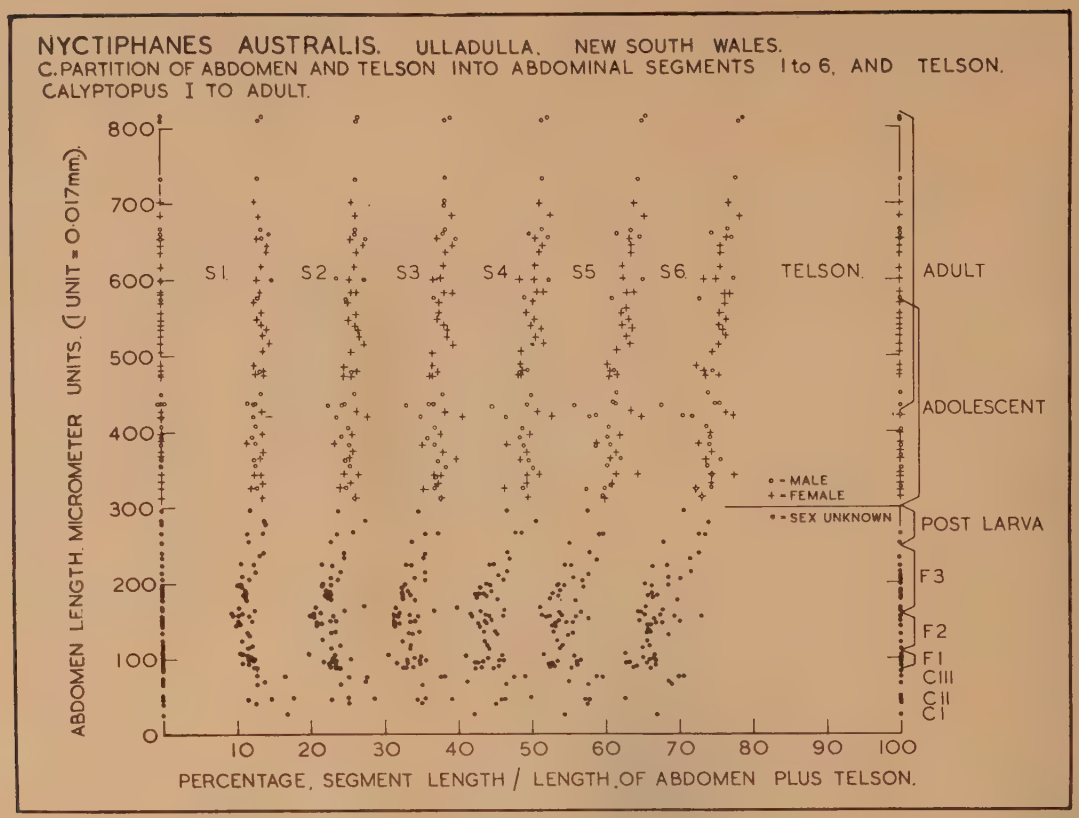


Fig. 16. *Nyctiphanes australis,* partition of abdomen length and telson into segments; and developmental phases.

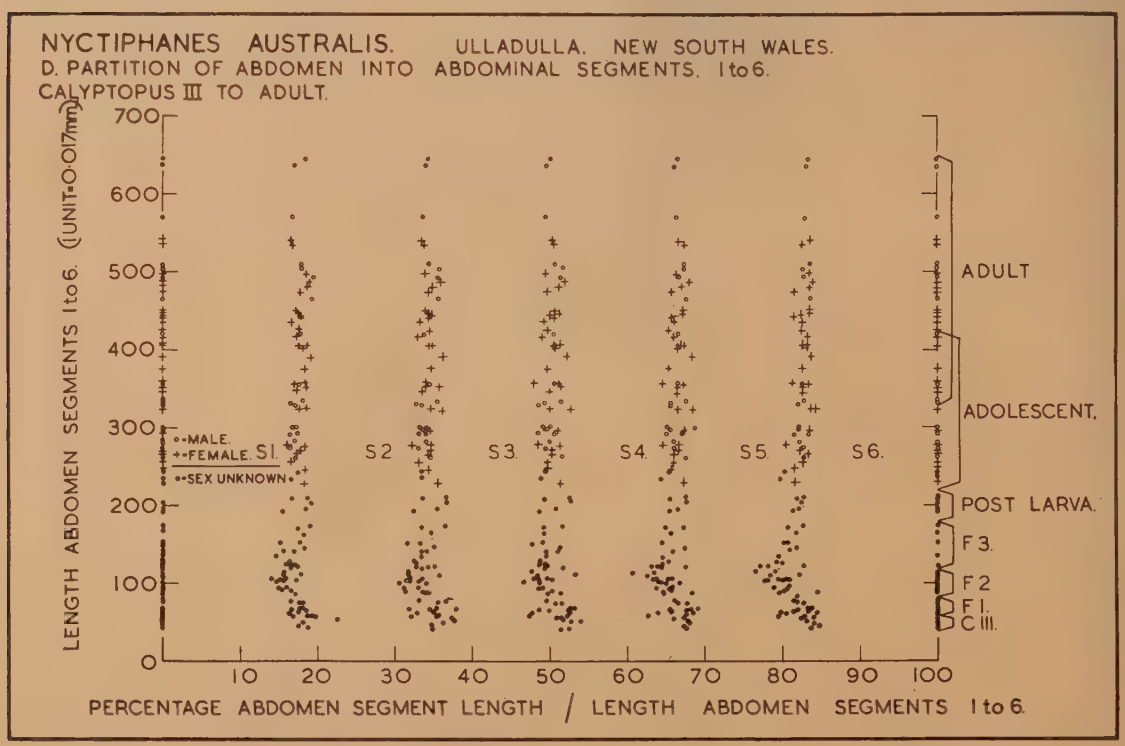


Fig. 17. *Nyctiphanes australis,* partition of abdomen length into segments; and developmental phases.

4. FUNCTION, FORM, DEVELOPMENT AND GROWTH IN THE EUPHAUSIACEA.

(a) FUNCTION.

No sequential experimental study of a Euphausiid has yet been made which would give a clearly defined picture of the emergence of the various functions of the organism; but a reasonably clear inferential picture is obtainable from very limited studies of the living animals, and from the various detailed morphological and developmental studies which have accumulated. An outline of the major development of some of the major functions is as follows:

(i) Locomotion. At first by means of cephalic appendages assisted by movements of the abdomen as a whole, later this is aided further by movements of the developing pleopods; in the mid and later stages cephalic locomotion ceases and is replaced by the use of the developed abdomen and its appendages; in the adult the latter is combined with the use of the thoracic appendages, chiefly of the exopods of the limbs.

(ii) Respiration. At first presumably generalized through the cuticle, later through the developed gills.

(iii) Nutrient intake. The organism appears to be non-feeding in the stages immediately following hatching, while the setose condition of the mouthparts (particularly of the maxillae) strongly suggest filter-feeding in the intermediate stages. As the thoracic limbs develop and become setose a net-like food basket is formed in some genera, e.g. *Euphausia* and *Nyctiphanes*. This is presumed to be efficient in the collection and storage of detritus and small elements of the plankton. In other genera, e.g. *Nematoscelis, Stylocheiron, Nematobrachion, Tessarabrachion,* and some species of *Thysanoessa,* semi-raptorial limbs develop.

(iv) Fat metabolism and storage. Little is known of the processes of fat metabolism in the Order, but it is a matter of observation that fat storage increases as the temperature decreases, until in high latitudes with the accompanying very low temperatures an appreciable proportion of the bulk of the organism is made up of fats in storage. Even within the same species, e.g. *Nyctiphanes australis,* in which fat storage is of a low order, ether extracts indicate a difference in the amount of fat stored at the same time of the year, when the northern part of the range is compared with the southern. In the case of *Thysanoessa gregaria* the difference is well marked, specimens taken in late summer, in latitude 34° S., yielding approximately 3 to 4 per cent. by volume of ether extracted oil, those from Bass Strait in latitude 40° S. yielding between 6 and 8 per cent. I have found no estimations of fresh material of *Euphausia superba;* but ether extracts of adult material stored in formalin from the B.A.N.Z.A.R.E. plankton indicated amounts lying between 12 and 15 per cent. by volume. Like extracts of *Thysanoessa macrura* from the same source were between 10 and 12 per cent. These figures are crude but they indicate that a significant part of the bulk of the organism is represented by fats in storage, and suggest that this factor must be taken into account when interpreting growth and development in Euphausiid species.

(v) Reproduction. The gonads are present as fine tubes early in the furcilia stages of *N. australis,* becoming folliculated in the late post-larval instars. From this point their development is rapid with the external sex processes roughly keeping pace. The only detailed work on the subject now is that of Bargmann (1945) on *Euphausia superba.* That author stresses the fact that "undue importance must not be attached to size as an indication of maturity."

(b) FORM.

The only gross change of form is that due to the emergence of the abdomen in the transition from the metanauplius to the first calyptopis stage. Minor changes include the segmentation of the abdomen, and telson in the calyptopis phase; the emergence of the eyes in the transition from the calyptopis to the furcilia stage; the progressive emergence of the pleopods and primary development of the thoracic appendages and gills during the furcilia phase; the subsequent elaboration of the thoracic appendages, and of the secondary sexual characteristics in the later phases. None of these changes are metamorphoses in the sense of a reorganization occurring during a resting period of the organism, and there is no corresponding, abrupt change of form.

(c) DEVELOPMENT AND GROWTH.

Although the intervention of ecdysis gives an impression of development through a series of short leaps, in reality development is a continuous process, the form of one instar being laid down in that preceding. The process is such that there is no complete standstill in the development of any part of the organism although the growth rate may slow down in one major section or in one set of appendages as compared with another; e.g., the slowing down in the development of the thoracic appendages during the period of rapid growth of the abdomen. It follows from this that the amount of growth of the thoracic appendages during the calyptopis and furcilia phases will depend partly on the length of time for which the instars persist. Other factors, one of which is temperature, may modify this. In the case of *Euphausia superba* there is such an early appearance of thoracic appendages. It has been speculated that the genus *Euphausia* is the youngest genus of the Order, and that *Euphausia superba* is one of the most recent species, and that the early development of the thoracic appendages lends support to the hypothesis that in the Euphausiacea continuous development is giving way to

a more marked metamorphosis (see John 1936, and Einarsson 1945). Since a comparison of the growth of parts in similar larval phases of various species of the Euphausiacea on such a time basis has not yet been made, it is perhaps premature to invoke the aid of such an abstraction to explain these differences in the development of species and genera of the Euphausiacea.

Perhaps a useful view of the process of development is that it is the visible, morphological expression of the total increase in complexity and organization. As such it is part of a larger integrative field which includes growth. In this view development would proceed at a composite rate for the whole, and at different but related rates for the parts, each rate possibly proportional to the distance to be covered in achieving the final form of the whole and of the parts. Growth itself, proceeding at sets of rates proportional to the distance from the mature size (Brody 1945, p. 245), may or may not be in step with development, depending externally on environmental factors; e.g., temperature, the presence of adequate nutrients and trace elements, and so on; and internally on the presence of genes controlling reaction rates (Needham 1942, p. 392) and other factors.

In the case of the Euphausiacea, although development is a continuous process, the greater part of growth increases occur in the normal crustacean manner at ecdyses, and is so a step-like process. Consequently the external form apparent in an instar is that revealed at one ecdysis and persisting to the next. During this period the form of the next instar is laid down. If the rates of development of the whole, or of parts, and the rates of growth are in step, one would expect to find individuals revealing corresponding forms at the same sequential instars, with a greater or lesser number deviating as environmental conditions varied for each individual (or as controlling genic field patterns varied), i.e. "dominant" instars would be present, becoming less apparent as the determining conditions varied. Such a process is evident in the furcilia phase of the various species.

5. THE FURCILIA PHASE IN THE EUPHAUSIACEA.

(Tables 14 to 17, Figs. 4 to 17.)

Adopting the concept of dissociability, or disengagement of growth and differentiation (Needham 1942, pp. 506-531), i.e., that the two are morphogenetically separable processes; and accepting as facts, firstly that the increase in differentiation (and hence of development) which occurs during a crustacean instar is manifested at the following ecdysis, and secondly that growth is a step-like phenomenon, likewise manifest at ecdysis, it is reasonable to assume that the form of instars of the earliest stages of individuals of a species will not differ greatly. It could be expected, further, that once the period of simple differentiation were past, such variation would tend to increase, with the exception that an environment common in all respects would act at least as a partial brake on variation. A prime factor tending to variability would be small differences in the amount of initial nutrient material packed into the egg.

In the case of the Euphausiacea such a progressive disengagement of differentiation and growth is evident to a greater or lesser extent in the various species. Incidentally, this is reflected by the amount of agreement and disagreement on nomenclature between the workers on larval development. For instance, there is uniformity of agreement in the recognizing and naming of the naupliar, and calyptopis phase, and of their respective stages; but at that point agreement stops. The stages of the furcilia phase are a matter of controversy, increased by the fact that experimental work on larval development is so difficult under land-based laboratory conditions that little has been carried out. In addition, the observed course of larval development from heterogeneous samples has been based on inadequate material in the majority of the species which have been examined. Even in the case of *Euphausia superba*, Fraser (1936), Bargmann (1945), and of *Nyctiphanes australis* in the present report, it is doubtful if the material which has been examined is either sufficient in numbers, or collected with sufficient sampling rigour to yield information of statistical value.

The present position is that, while some measure of agreement has been arrived at regarding the limits of the furcilia phase as a whole, the numbers of stages which are recognized vary from species to species and from genus to genus, since the stages themselves are named afresh in each species. Thus the stages have ceased to become a framework of classification, but are regarded as attributes of the species. This is due in part to a reaction from the obviously unsuitable method adopted by earlier authors of nominating each instar form (based on pleopod emergence) as a separate furcilia stage; and in part, as discussed earlier, to the use of the word "dominant" to denote the instar most frequently found in a set of plankton samples.

A return to the use of the furcilia stages as a framework of classification in the furcilia phase appeared desirable. Consequently I examined the published accounts of furcilia phase development to supplement the studies mentioned earlier in this report, and considered as a result, that the three-stage furcilia classification with a suitable notation to denote instar forms (as described in Section F, part 2 (b); Nomenclature), could be applied to the development of the furcilia phase in all species which have been analysed so far.

The furcilia phase as defined in Section F, part 2 (h) is regarded as the phase in development during which the abdomen is differentiated in detail to act as a locomotor organ. Development of the abdomen is regarded as proceeding from the anterior segments to the posterior. The major processes in time sequences are:

Furcilia 1. The development of the pleopods as non-functional rudiments.

Furcilia 2. The development of the pleopods, and of their accompanying musculature, as functional elements.

Furcilia 3. The elaboration of the telson and the final definition of the pleopods.

The three furcilia stages comprising the furcilia phase proposed in this report include the following stages recognized by other authors.

Furcilia 1 equals: furcilia 1 to 6 of Lebour (1926d); furcilia 1 and 2 of Rustad (1930); early furcilia of Ruud (1932); furcilia 1 *(E. superba)* of Fraser (1936); furcilia 1 *(E. frigida, vallentini, triacantha, longirostris* and *spinifera*) of John (1936); furcilia 1, and part of furcilia 2 (in the case of *Thysanopoda aequalis, Thysanoessa raschii, inermis, macrura,* and *gregaria)* of Gurney (1942); furcilia 1 and 2 (part) of Einarsson (1945); furcilia stage 1 of Boden (1950), *E. pacifica*; and of Boden (1951), *Nyctiphanes simplex.*

Furcilia 2 equals: furcilia 7 to 14 of Lebour (1926d); furcilia 3 to 6 *(E. frigida)* of Rustad (1930); Intermediate furcilia of Ruud (1932); furcilia 2 of Fraser (1936); furcilia 2, 3 (part) and 4 (part) of John (1936, table 2, p. 258); furcilia 2 (part), 3, and 4 (part) of Gurney (1942, p. 173); furcilia 2 (part) and furcilia 3 of Einarsson (1945); furcilia, stage 2 of Boden (1950 and 1951).

Furcilia 3 equals: Cyrtopia (part) of Lebour (1926d); early cyrtopia stages of Rustad (1930); late furcilia and early cyrtopia of Ruud (1932); furcilia 3 to 6 of Fraser (1936); furcilia 3 (part), 4 (part), and 5 to 7 of John (1936); furcilia 4 (part) and 5 of Gurney (1942); furcilia 4 to 7 and 8 to 10, depending on the species, of Einarsson (1945); furcilia stages 3 to 7 of Boden (1950), and 3 to 6 of Boden (1951).

In the majority of the species the respective rates of differentiation of abdomen and telson are such that the final development of the telson and its armature form a clear-cut third stage accompanied only by minor changes in the pleopods, generally in the direction of the addition of extra setae, particularly on the endopod. In some species (viz., *Pseudeuphausia latifrons* and *Thysanopoda aequalis*), the rate of development of the

TABLE 16.

A CONSPECTUS OF INSTARS IN THE FURCILIA PHASE
EUPHAUSID GENERA AND SPECIES

Instar	(a) Thysanopoda								Stage
	aequalis	acutifrons	cristata	orientalis	tricuspidata	microphthalma	pectinata	cornuta	
	Number of Telson Spines, Terminal								
Op	7				7				
1N									
2N	5				7				
3N		7	7	7	7	7	7		Furcilia I
4N								?	
5N	5								
1S									
1S1N									
1S2N									
1S3N					7				
1S4N									
2S									
2S1N									Furcilia II
2S2N	3				7				
2S3N					7				
3S									
3S1N									
3S2N		7	7	7	7	7	7		
4S									
4S1N	3/2				7			?	
5S.7sp.A		7	7	7		7	7	?	
	Number of Terminal Spines, Lateral								
5S.7sp.B		3/2			3/2	2			
5S6sp.		2							
5S5sp.	2	2							
5S4sp.		2							
5S3sp.	2	2	2						Furcilia III
5S2sp.									
5S1sp.									
	Reference								
	Lebour	Einarsson	Gurney	Hansen	Tattersall	Einarsson	Einarsson	Einarsson	

TABLE 16 (continued).

FURCILIA INSTARS

Instar	(b) Meganyctiphanes norvegica	(c) Nyctiphanes australis			(d) Pseudeuphausia latifrons	(e) Euphausia											Phase
			simplex	couchii		superba	recurva	brevis	krohnii	vallentini	frigida	triacantha	longirostris	spinifera	similis	pacifica	
						Number of Telson Spines, Terminal											
OP	7	7		7	7/5	7	7		7					7	7	7	
1N	7	7	7	7	5/3		7	7	7				7	7	7	7	
2N	7	7	7	7	5/3	7	7									7	
3N	7	7	7	7	5/3	7	7				7			7	7	7	Furcilia I
4N	7	7		7		7				7	7	7					
5N		7				7					7	7					
1S																	
1S1N		7			3												
1S2N		7			5/3									7			
1S3N	7	7	7	7	3	7	7						7	7	7	7	
1S4N		7					7	7	7							7	
2S		7															
2S1N		7			3	7											Furcilia II
2S2N	7	7	7	7	3/1	7	7										
2S3N	7	7		7		7	7										
3S		7															
3S1N		7			3/1	7	7										
3S2N	7	7	7	7	1	7	7			7	7					7	
4S		7				7											
4S1N		7	7	7		7	7			7	7	7	7	7	7	7	
5S.7sp.A	7	7	7	7		7			7	7	7	7	7				
						Number of Spines, Lateral											
5S7sp.B	3	3				3	3	3	3	3			3	3	3	3	
5S6sp.	3	3	3			3					3	3	3			3	
5S5sp.	3	3	3	3	3	3			3	3	3	3	3	3	3	3	Furcilia III
5S4sp.		3	3			3				3	3	3	3			3	
5S3sp.	3/2	3	3	3	3	3	3	3	3	3	3	3	3	3/2	3	3	
5S2sp.		3	3			3				3	3	3				3	
5S1sp.		3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	
						Reference											
	Einarsson	Sheard	Boden	Einarsson	Gurney Sheard	Fraser	Sheard	Gurney	Einarsson	John	John	John	John	John Sheard	Sheard	Boden	

telson is continuous so that telson changes such as the progressive loss or alteration of the terminal spines are initiated in the early furcilia stages. The concluding operations of this process occur however in the well-marked third stage, in which the posterior lateral spines are present.

The characteristics of the instars of the furcilia stages in the species so far analysed are shown in Tables 16 and 17. It will be noted that pleopod emergence is regarded as taking precedence over reduction in the terminal spines of the telson; and both, over the reduction of the larval post-lateral spine, the central one of the three.

In Table 17 this grouping of instars has been followed for the species whose development in this phase has been recorded with some degree of reliability. The number of instars recorded in each stage are noted. It will be seen that the number of instars which have been found in each stage varies with the species. This does not imply that each individual passed through the whole set of instars. Instead, the operation of the general rule that pleopods non-setose in one instar are setose in the next ensures that the number of instars passed through by an individual in each furcilia stage is limited. For example, in the case of the massed sample of *Nyctiphanes australis* recorded in Fig. 4, although six possible instars occur in furcilia stage 1, the number of instars likely for any one individual is two. In furcilia stage 2, the total number of different instars possible is fourteen, but the strict developmental sequence of individuals is limited to from one to three successive instars. In furcilia stage 3, with four possible instars (seven if the aberrant even numbered terminal spine instars are counted), the number of successive instars likely varies from two to four.

TABLE 16 (continued).

FURCILIA INSTARS

Instar	(f) Thysanoessa					(g) Nematoscelis				(h) Stylocheiron		Phase
	raschii	inermis	longicaudata	macrura	gregaria	microps	megalops	difficilis	suhmii	abbreviatum	longicorne	
Number of Telson Spines, Terminal												
OP	7	7	7	7	7			7	6	7	7	
1N	7	7			7	7		7	6	7	7	
2N	7	7					7	7	6			Furcilia I
3N	7	7			7							
4N	7	7										
5N	7	7	7	7	7			7				
1S												
1S1N												
1S2N									6	7	7	
1S3N						7						
1S4N	7	7			7							
2S												
2S2N												Fucilia II
2S3N	7	7			7		7	7	6			
3S												
3S1N												
3S3N	7	7			7			7	6	7	7	
4S					7							
4S1N	7	7			7	5/3		7				
5S.7sp.A	7	7	7	7	7			7			7	
Number of Telson Spines, Lateral												
5S.7sp.B	3	3	3		3		3	3				
5S5sp.	3	3	3	3	3		3			3	2	
5S4sp.	3								3			Furcilia III
5S3sp.	3	3	3	3	3	3/2		3				
5S2sp.												
5S1sp.	3	3	3	3	3							
Reference	Einarsson	Einarsson	Einarsson	Rustad	Sheard	Lebour	Frost	Sheard	Gurney	Lebour	Frost	

The variation in the total number of instars in each stage from the analysis of samples of *N. australis* taken from different plankton hauls is recorded in Figs. 5 to 10. Reference to the same set of figures shows that a misleading idea of the "dominant" instar may be gained from such partial samples. For instance, if a mass sample of *N. australis* were largely contributed to by that analysed in Fig. 9, instars 3N and 4N would be regarded as dominant instars of the first furcilia stage, with 3N as the most probably dominant; instars 0N, 1N, and 5N would be of little account; and instar 2N, a minor alternative. Reference to Fig. 4 indicates that this analysis might be incorrect; although there is some indication that the most favoured instar is 3N, with 5N a rarity. The use of the term "dominant" with regard to 3N would be however a rather unwise use of the term.

In the case of the second furcilia stage of mixed setose and non-setose pleopods, the instar 4S1N would be chosen with little hesitation as the dominant instar in Fig. 9. Reference to Fig. 4 would not uphold this conclusion. In passing, it may be indicated that Fig. 4 is itself a statistically unreliable sample since the addition of sub-samples, themselves not random, do not necessarily ensure a random mass sample. Fig. 4 records the bare facts that 27 instars have been found in the furcilia phase of *N. australis* and that the development of the individuals may pass along one or another of a number of paths. It also indicates a grouping of size ranges of certain instars, corresponding roughly to the respective furcilia stages.

It is possible, however, that the reduced number of instars which have been recorded for some species may be due to the fact that other instars do not occur, i.e., that in some there is a closer engagement between differentiation and growth in the sense of Needham (1942). A lesser number of instars have been found in oceanic species than in neritic (and as a subdivision of these categories) in cold water than warm water species. The present view is summarized by Einarsson (1945, p. 13) in the following words: "We therefore think it necessary to seek the explanation in the varying natural conditions of the coastal waters as contrasted with the more stable and uniform conditions of oceanic waters. The data given by Fraser's (1936) investigations suggest that greater variability may be a local phenomenon."

TABLE 17.

EUPHAUSIACEAN CALYPTOPIS AND FURCILIA PHASES

Size and Range; Number of Instars Recorded

Species	Calyptopis			Furcilia I		Furcilia II		Furcilia III	
	I	II	III	Size (mm.)	Instars	Size (mm.)	Instars	Size (mm.)	Instars
M. norvegica	1	1·5	2·5	2·8–3·5	5	3·8–5·0	5	5·5–8·5	4
N. australis	0·8–1·4	1·4–1·9	1·6–2·4	1·9–3·3	6	2·7–4·0	14	3·6–6·0	7
N. couchii				2·5–3·5	5	3·2–4·3	6	4·3–4·8	3
N. simplex	0·99–1·31	1·35–1·75	1·8–2·26	2·4–2·9	3	3·3–4·5	5	4·2–6·0	4
P. latifrons		1·2–2·0	2	2·3–2·6	4	2·5–3·5	7	3·0–5·6	3
E. superba	1·3–1·9	2·1–3·3	3·2–4·8	3·5–6·5	6	4·0–7·9	9	5·8–15·5	7
E. recurva				2·2–3·1	4	2·9–3·6	7	3·5–6·0	3
E. brevis					1		1		
E. krohnii				2·5–3·5	2	3·0–4·7	2	3·7–7·0	4
E. vallentini		1·6–1·8	2·5–2·8	3·2–4·0	1	4·5–5·1	3	5·4–9·3	5
E. frigida		1·5–1·8	2·5–2·9	3·8–3·4	3	4·2–5·7	2	5·5–9·6	6
E. triacantha		1·9–2·3	3·0–3·6	4·0–5·3	2	5·0–7·7	3	6·5–11·4	6
E. longirostris		2·0–2·1	3·3–3·6	4·2–4·7	1	5·0–6·3	3	6·4–8·5	5
E. spinifera		1·9–2·4	2·6–3·3	3·0–5·3	3	5·0–6·0	3	6·0–9·5	4
E. similis				3·2–3·4	3	3·5–3·9	2	4·0–7·0	4
E. pacifica	1·2	1·9	2·5	3·0–3·2	4	3·5–4·1	5	3·6–6·5	5
T. raschii	1·0–1·6	1·8–2·0	2·4–2·5	3·0–3·9	6	3·8–5·2	5	5·0–9·0	5
T. inermis	1	1·8	2·5	3·0–3·6	6	3·8–5·3	5	5·0–7·0	4
T. longicaudata	1	1·8	2·5	3·2–3·7	2	4·0	1	4·5–5·8	4
T. macrura				3·0–3·5	2	3·7	1	3·7–7·0	3
T. gregaria	0·9–1·4	1·4–1·6	2·0–2·5	2·5–3·2	4	2·6–3·7	6	2·8–5·3	4
N. microps					1		2		1
N. megalops					1		1		2
N. difficilis	1·6		2·0–2·0	2·4–3·5	4	2·8–4·0	4	3·0–5·5	2
S. suhmii				2·2–2·4	3	2·4–2·8	3	3·0	1
S. abbreviatum				2·1	2	2·8–3·2	3	3·0–3·3	1
S. longicorne					2		3		1
T. aequalis					3		2		2
T. acutifrons		3·5–3·8	4·5–4·7	5·8–5·9	1	6·8–7·8	2	9·0–11·5	5
T. cristata					1		2		1
T. orientalis					1		2		3
T. tricuspidata					3		5		1
T. microphthalma					1		2		1
T. pectinata					1		2		?
T. cornuta					1		2		?

It is true that temperature (which could be regarded with some certainty as an operating factor) shows less variation in a given oceanic water mass than in neritic waters. (Also there is likelihood of a lesser concentration of essential trace elements, resulting from run-off from the land, in oceanic as opposed to neritic waters, where in addition the scour of the bottom currents offers better opportunity for the solution of such factors from sea-bottom deposits.) It must be pointed out in assessing the results of this difference, that the larvae of the Euphausiacea exhibit a considerable amount of vertical movement diurnally and favour different depths in different phases of development and thus, even in ocean waters, the swarms may be expected to encounter some variation in conditions. In spite of this objection the tentative explanation given by Einarsson (1945) may be correct. The case of the variation in *Euphausia superba*, generally reckoned an oceanic species, may not be an objection as it inhabits the region of the pack ice, which simulates neritic conditions in some respects. A further explanation may lie in genetic differences as mentioned earlier, but no experimental evidence exists in that regard concerning the Euphausiacea. With this as with other aspects of the development and growth of the Euphausiacea little real progress can be made in the absence of experiment.

G. ACKNOWLEDGMENTS.

I wish again to express my indebtedness to the late Professor T. Harvey Johnston, and to Sir Douglas Mawson, for making the B.A.N.Z.A.R.E. collections available; and to my colleagues in the Division of Fisheries, C.S.I.R.O., for their interest and assistance, notably of those in the Technical Branch for final preparation and photographing of the figures.

In addition I am indebted to Mr. H. M. Hale, Director of the South Australian Museum, for providing laboratory space and advice in the early stage of the project, and to Professor H. Waring, of the Department of Zoology, University of Western Australia, for like services in the final stages.

H. Appendix.

TABLE 14.

NYCTIPHANES AUSTRALIS

Biological Data, Growth Partition Series

Series No.	Instar	Phase	Data
1	Nauplius	Nauplius	Moulting to Meta-nauplius
2	Meta-N	Meta-N	„ „ Calyptopis I
3	CI	Calyptopis	„ „ Calyptopis II
4	CI		„ „ „ „
5	CII		„ „ Calyptopis III
6	„		„ „ „ „
7	„		„ „ „ „
8	„		„ „ „ „
9	CIII		„ „ O.P.
10	„		„ „ 1N
11	„		„ „ 3N
12	„		„ „ 3N
13	OP		„ „ 4N
14	1N		„ „ 1S3N
15	„		„ „ 1S3N
16	„		„ „ 1S4N
17	2N		„ „ 2S3N
18	3N	Furcilia I	„ „ 3S1N
19	„		„ „ 3S2N
20	„		„ „ 3S2N
21	„		„ „ 3S2N
22	4N		„ „ 4S1N
23	„		„ „ 4S1N
24	„		„ „ 4S1N
25	1S3N		„ „ 4S1N
26	2S2N		„ „ 4S1N
27	2S3N		„ „ 5S7sp.A
28	3S2N		„ „ „ Photophore at base of Pleopod 1
29	„		„ „ „ „ „ „ „
30	„		„ „ „ „ „ „ „
31	4S1N		„ „ 5S7sp.B „ „ „ „
32	„		„ „ „ „ „ „ „
33	„	Furcilia II	„ „ „ „ „ „ „
34	5S7sp.A		„ „ 5S5sp. Photophore at base of Leg 1 and Pleopod 4
35	„		„ „ „ „ „ „ „
36	„		„ „ „ „ „ „ „
37	„		„ „ „ „ „ „ „
38	„		„ „ „ „ „ „ „
39	„		„ „ „ „ „ „ „
40	„		„ „ „ „ „ „ „
41	„		„ „ „ „ „ „ „
42	„		„ „ „ „ „ „ „
43	5S7sp.B		„ „ 5S5sp. „ „ „ „
44	„		„ „ 5S3sp. „ „ „ „
45	5S5sp.		„ „ 5S3sp. Gills developed on Legs 1 to 4
46	„		„ „ „ „ „ „ „
47	„		„ „ „ „ „ „ „
48	„		„ „ 5S1sp.3P.L. „ „ „ „
49	„		„ „ „ „ „ „ „
50	5S3sp.	Furcilia III	„ „ „ Antenna differentiated.
51	„		„ „ „ „ „
52	„		„ „ „ „ „
53	„		„ „ „ „ „
54	„		„ „ „ „ „
55	5S1sp.3P.L.		Photophore at base of Leg 6. Antennal scale fully formed, Palp of Mandible, three segmented.
56	„		„ „ „ „ „
57	„		„ „ „ „ „
58	„		„ „ „ „ „
59	„		„ „ „ „ „
60	„		„ „ „ „ „
61	„		
62	1sp.2P.L.	Post-larva	Thoracic limbs showing progressive development in this series, this development proceeds during the following stages until completed at a length of about 12 mm. in the ♀ and 10 mm. in the ♂
63	„		„ „ „ „ „
64	„		„ „ „ „ „
65	„		
66	„		
67	♀		Ovaries 0·9 mm.
68	♂		Gonad 0·5 mm.
69	♂		Gonad 0·5 mm.
70	♀		Gonads developing, length 1·3 mm.
71	♀		„ „ „ 1·0 mm.
72	♀		„ „ „ 1·1 mm.
73	♂		Cop. organs not developed. Gonads 0·75 mm.
74	♂		Cop. organs developing. Gonads 0·9 mm.
75	♂		„ „ „ Gonads 0·7 mm.
76	♀		Gonads developing 0·75 mm.
77	♀		„ „ 0·6 mm.
78	♂		Cop. organs developing. Gonads 0·9 mm.
79	♂		„ „ „ Gonads 1·0 mm.
80	♀		Gonads developing. No ova.
81	♀		„ „ 2·1 mm. Ova 0·1 mm.
82	♂		Cop. organs developing. Gonads 1·0 mm.
83	♂		„ „ „ Gonads 0·4 mm.
84	♂		„ „ „ Gonads 1·0 mm.
85	♂		„ „ „ Gonads 1·1 mm.
86	♂		Cop. organs not developing. Gonads 0·6 mm.
87	♀		Gonads 1·2 mm.
88	♂		Cop. organs developing. Gonads 0·95 mm.
89	♂		Egg sac full. Gonads 2·0 mm. Ova 0·1 mm.
90	♂		Cop. organs developing. Gonads 2·5 mm.
91	♂		Cop. organs developing. Gonads 2·0 mm.
92	♀		Egg sac full eggs. 0·35 mm. Gonads 1·5 mm.
93	♀		„ „ „ „ Eggs 0·1 mm.
94	♀		No egg sac. Gonads 1·8 mm. Empty.
95	♀		No egg sac. Gonads 3·0 mm. Ova 0·35 mm.
96	♀		No egg sac. Gonads 1·7 mm. Empty.
97	♀		No egg sac. Gonads 1·8 mm. Ova 0·15 mm.
98	♀		No egg sac. Gonads 3·0 mm. Ova 0·26 mm.
99	♀		Egg sac full. Gonads 2·0 mm. Empty
100	♀		No egg sac. Gonads 3·0 mm. Ova 0·35 mm. ripe
101	♀		Egg sac full. Eggs 0·4 mm. Gonads 2·3 mm. Ova 0·15 mm.
102	♂		Cop. organs developed. Gonads 3·0 mm. ripe.
103	♀		Egg sac full. Gonads 2·0 mm. Ova 0·1 mm.
104	♀		Egg sac full. Gonads 1·5 mm. Empty.
105	♀		Egg sac full. Gonads 1·9 mm. Ova 0·1 mm.
106	♀		Egg sac full. Eggs 0·4 mm. Gonads 3·0 mm. Empty.
107	♂		Cop. organs not mature
108	♂		No egg sac. Gonads 3·2 mm. Ova 0·28 mm.
109	♀		No egg sac. Gonads 3·0 mm. Eggs 0·2 mm.
110	♀		Egg sac full. Eggs 0·4 mm. Gonads 1·6 mm. Empty.
111	♂		Gonads 3·1 mm. Empty.
112	♂		Gonads 3·0 mm. Empty.
113	♀		Egg sac full. Eggs 0·45 mm. Gonads 2·7 mm. Ova 0·2 mm.
114	♀		Egg sac full. Eggs 0·45 mm. Gonads 1·8 mm. Ova 0·1 mm.
115	♂		Gonads ripe 3·5 mm. Ova 0·3 mm.
116	♀		Egg sac full. Gonads 2·5 mm. Ova 0·2 mm.
117	♀		Egg sac full. Eggs 0·4 mm. Gonads 2·5 mm. Ova 0·2 mm.
118	♂		Gonads spent.
119	♀		Egg sac full. Eggs 0·4 mm. Gonads 2·8 mm. Ova 0·25 mm.
120	♂		Gonads spent.
121	♂		Gonads ripe. 3·0 mm.

TABLE 15.

NYCTIPHANES AUSTRALIS

Growth Partition Data

All lengths in micrometer units (1 unit = 0·017 mm.)
(B) Segment length/total length, percentage
(C) Segment length/abdomen length, percentage
(D) Segment length/abdomen segments 1–6, percentage

No.	Instar	T.L.	C.L.	A.L.	A.S1	A.S2	A.S3	A.S4	A.S5	A.S6	T	A.S1–S6
1	Nauplius	23	23									
	B		100									
2	Meta-N	45	30	15								
	B		66·7	33·3								
3	Cal. I	65	41	24	4	3	3	3	3		8	
	B		63·1	37·9	6·1	4·6	4·6	4·6	4·6		12·3	
	C				16·7	12·5	12·5	12·5	12·5		33·3	
4	Cal. I	65	41	24	4	3	3	3	3		8	
	B		63·1	36·9	6·1	4·6	4·6	4·6	4·6		12·5	
	C				16·7	12·5	12·5	12·5	12·5		33·3	
5	Cal. II	83	43	40	5	5	4	4	5		17	
	B		51·7	48·3	6·0	6·0	4·8	4·8	6·0		20·5	
	C				12·5	12·5	10·0	10·0	12·5		42·5	
6	Cal. II	88	41	47	6	5	5	5	6		20	
	B		46·6	53·4	7·9	5·6	5·6	5·6	7·9		22·4	
	C				14·6	10·4	10·4	10·4	12·5		41·7	
7	Cal. II	88	42	46	8	5	5	5	6		17	
	B		47·7	52·3	9·0	5·6	5·6	5·6	7·9		19·1	
	C				17·4	10·8	10·8	10·8	13·0		37·0	
8	Cal. II	89	45	44	5	5	5	5	5		19	
	B		50·5	49·5	5·6	5·6	5·6	5·6	5·6		21·5	
					11·4	11·4	11·4	11·4	11·4		42·5	
9	Cal. III	116	53	63	8	7	7	7	7	7	20	43
	B		45·9	54·1	6·9	6·0	6·0	6·0	6·0	6·0	17·2	36·9
	C				12·7	11·1	11·1	11·1	11·1	11·1	31·7	68·3
	D				18·6	16·3	16·3	16·3	16·3	16·3		
10	Cal. III	123	50	73	12	8	8	8	8	9	20	53
	B		40·6	59·4	9·8	6·5	6·5	6·5	6·5	7·4	16·3	43·1
	C				16·4	10·9	10·9	10·9	10·9	12·3	27·4	72·6
	D				22·6	15·1	15·1	15·1	15·1	17·0		
11	Cal. III	124	56	68	8	8	8	7	8	7	22	46
	B		42·5	57·5	6·4	6·4	6·4	5·6	6·4	5·6	17·4	36·8
	C				13·8	13·8	13·8	12·1	13·8	12·1	20·7	79·3
	D				17·4	17·4	17·4	15·2	17·4	15·2		
12	Cal. III	132	60	72	9	9	9	7	8	8	22	50
	B		44·6	55·4	6·9	6·9	6·9	5·5	6·2	6·2	16·8	38·6
	C				12·5	12·5	12·5	9·7	11·1	11·1	30·6	69·4
	D				18·0	18·0	18·0	14·0	16·0	16·0		
13	O.P.	144	56	88	11	10	8	8	9	10	32	56
	B		39·2	60·8	7·6	6·9	5·6	5·6	6·2	6·9	22·2	38·6
	C				12·5	11·4	9·1	9·1	10·2	11·4	36·4	63·6
	D				19·6	17·8	14·3	14·3	16·1	17·8		
14	1N	146	60	86	11	9	9	9	9	9	30	56
	B		41·6	58·4	7·5	6·1	6·1	6·1	6·1	6·1	20·4	38·0
	C				12·8	10·5	10·5	10·5	10·5	10·5	34·9	65·1
	D				19·6	16·1	16·1	16·1	16·1	16·1		
15	1N	148	59	89	11	9	9	9	9	10	32	57
	B		38·8	60·2	7·4	6·1	6·1	6·1	6·1	6·8	21·6	38·6
	C				12·4	10·1	10·1	10·1	10·1	11·2	36·0	64·0
	D				19·3	15·8	15·8	15·8	15·8	17·5		
16	1N	157	62	95	11	11	11	10	10	10	32	63
	B		39·4	60·6	7·0	7·0	7·0	6·4	6·4	6·4	20·4	42·0
	C				11·6	11·6	11·6	10·5	10·5	10·5	33·7	66·3
	D				17·5	17·5	17·5	15·9	15·9	15·9		

TABLE 15 (continued).

No.	Instar	T.L.	C.L.	A.L.	A.S1	A.S2	A.S3	A.S4	A.S5	A.S6	T	A.S1–S6
17	2N	148	57	91	10	9	9	9	10	12	32	59
	B		39·4	60·6	7·0	7·0	7·0	6·4	6·4	6·4	20·4	40·2
	C				11·6	11·6	11·6	10·5	10·5	10·5	33·7	66·3
	D				16·9	15·2	15·2	15·2	16·9	20·4		
18	3N	150	57	93	11	10	10	9	9	10	34	59
	B		37·9	62·1	7·3	6·7	6·7	6·0	6·0	6·7	22·7	39·4
	C				11·8	10·7	10·7	9·7	9·7	10·7	36·6	63·4
	D				18·6	16·9	16·9	15·2	15·2	16·9		
19	3N	154	55	99	12	10	10	10	10	12	35	64
	B		35·7	64·3	7·8	6·5	6·5	6·5	6·5	7·8	22·7	41·6
	C				12·1	10·1	10·1	10·1	10·1	12·1	35·5	64·5
	D				18·7	15·6	15·6	15·6	15·6	18·7		
20	3N	160	60	100	12	11	11	10	10	11	35	65
	B		37·5	62·5	7·5	6·9	6·9	6·2	6·2	6·9	21·9	40·6
	C				12·0	11·0	11·0	10·0	10·0	11·0	35·0	65·0
	D				18·5	16·9	16·9	15·4	15·4	16·9		
21	3N	160	61	99	12	13	10	10	10	11	33	66
	B		38·3	61·7	7·5	8·1	6·2	6·2	6·2	6·9	20·6	41·1
	C				12·1	13·1	10·1	10·1	10·1	11·1	33·3	66·7
	D				18·2	19·7	15·1	15·1	15·1	16·7		
22	4N	158	65	93	10	10	9	10	10	12	32	61
	B		41·3	58·7	6·3	6·3	5·7	6·3	6·3	7·6	20·2	38·5
	C				10·7	10·7	9·7	10·7	10·7	12·9	34·4	65·6
	D				16·4	16·4	14·7	16·4	16·4	19·7		
23	4N	166	63	103	12	12	12	11	10	11	35	68
	B		38·2	61·8	7·2	7·2	7·2	6·6	6·0	6·6	21·1	40·8
	C				11·6	11·6	11·6	10·7	9·7	10·7	34·0	66·0
	D				17·6	17·6	17·6	16·2	14·7	16·2		
24	4N	166	52	114	13	13	12	12	11	13	40	74
	B		31·6	68·4	7·8	7·8	7·2	7·2	6·6	7·8	24·1	44·4
	C				11·4	11·4	10·5	10·5	9·6	11·4	35·1	64·9
	D				17·6	17·6	16·2	16·2	14·9	17·6		
25	1S3N	172	66	106	11	10	11	11	11	12	40	66
	B		38·3	61·7	6·4	5·8	6·4	6·4	6·4	7·0	23·3	38·4
	C				10·4	9·4	10·4	10·4	10·4	11·3	37·4	62·6
	D				16·7	15·1	16·7	16·7	16·7	18·2		
26	2S2N	178	56	122	13	13	13	13	12	15	43	79
	B		31·6	68·4	7·3	7·3	7·3	7·3	6·7	8·4	24·1	44·3
	C				10·7	10·7	10·7	10·7	9·8	12·3	35·2	65·8
	D				16·5	16·5	16·5	16·5	15·2	19·0		
27	2S3N	194	60	134	15	15	15	15	14	14	46	88
	B		30·7	69·3	7·7	7·7	7·7	7·7	7·2	7·2	23·7	45·6
	C				11·2	11·2	11·2	11·2	10·4	10·4	34·4	65·7
	D				17·1	17·1	17·1	17·1	15·9	15·9		
28	3S2N	178	61	117	14	14	11	12	12	14	40	77
	B		34·5	65·5	7·8	7·8	6·2	6·7	6·7	7·8	22·5	43·0
	C				12·0	12·0	9·4	10·3	10·3	12·0	34·2	65·8
	D				18·2	18·2	14·3	15·6	15·6	18·2		
29	3S2N	208	74	134	15	15	14	13	13	18	46	88
	B		35·8	64·2	7·2	7·2	6·7	6·2	6·2	8·6	22·1	42·1
	C				11·2	11·2	10·4	9·7	9·7	13·4	34·3	65·7
	D				17·0	17·0	15·9	14·8	14·8	20·5		
30	3S2N	214	72	142	14	15	15	16	14	18	50	92
	B		33·9	66·1	6·5	7·0	7·0	7·5	6·5	8·4	23·4	42·9
	C				9·9	10·6	10·6	11·3	9·9	12·9	35·2	64·8
	D				15·2	16·3	16·3	17·4	15·2	19·6		
31	4S1N	202	71	131	16	15	15	14	13	18	41	90
	B		35·3	64·7	7·4	7·4	7·4	6·9	6·4	8·9	20·3	44·4
	C				11·5	11·5	11·5	10·7	9·9	13·7	31·3	68·7
	D				16·7	16·7	16·7	15·6	14·4	20·0		

TABLE 15 (continued).

No.	Instar	T.L.	C.L.	A.L.	A.S1	A.S2	A.S3	A.S4	A.S5	A.S6	T	A.S1–S6
32	4S1N	214	72	142	14	15	16	16	13	18	49	93
	B		33·6	66·3	6·5	7·0	7·5	7·5	6·5	8·4	22·9	43·4
	C				9·9	10·6	11·3	11·3	9·9	12·8	34·7	65·3
	D				15·1	16·1	17·2	17·2	15·1	19·3		
33	4S1N	220	70	150	18	17	16	16	15	23	45	105
	B		31·8	68·2	8·2	7·7	7·3	7·3	6·8	10·4	20·4	47·8
	C				12·0	11·3	10·7	10·7	10·7	15·3	30·0	70·0
	D				17·1	16·2	15·2	15·2	14·3	21·9		
34	7sp.A	220	76	144	15	16	15	14	14	20	50	94
	B		34·9	65·1	6·8	7·3	6·8	6·4	6·4	9·1	22·3	42·8
	C				10·4	11·1	10·4	9·7	9·7	13·9	34·7	65·3
	D				16·0	17·0	16·0	14·9	14·9	21·3		
35	7sp.A	228	72	156	18	18	18	18	18	24	42	114
	B		31·2	68·4	7·9	7·9	7·9	7·9	7·9	10·5	18·4	50·0
	C				11·5	11·5	11·5	11·5	11·5	15·4	26·9	73·1
	D				15·8	15·8	15·8	15·8	15·8	21·0		
36	7sp.A	228	72	156	18	18	18	15	18	27	42	114
	B		31·2	68·4	7·9	7·9	7·9	6·6	7·9	11·8	18·4	50·0
	C				11·5	11·5	11·5	9·6	11·5	17·3	26·9	73·1
	D				15·8	15·8	15·8	13·1	15·8	23·7		
37	7sp.A	230	80	150	18	16	16	15	15	20	50	100
	B		34·6	65·4	7·8	7·0	7·0	6·5	6·5	8·7	21·7	43·7
	C				12·0	10·7	10·7	10·0	10·0	13·3	33·3	66·7
	D				18·0	16·0	16·0	15·0	15·0	20·0		
38	7sp.A	232	83	149	15	16	16	18	16	20	48	101
	B		35·9	64·1	6·6	6·9	6·9	7·7	6·9	8·6	20·7	43·6
	C				10·1	10·7	10·7	12·1	10·7	13·4	32·2	
	D				14·8	15·8	15·8	17·8	15·8	19·8	47·5	
39	7sp.A	236	80	156	16	17	20	16	16	20	51	105
	B		33·8	66·2	6·8	7·2	8·5	6·8	6·8	8·5	21·6	44·6
	C				9·6	10·2	12·0	9·6	9·6	12·0	30·7	69·3
	D				15·2	16·2	19·0	15·2	15·2	19·0		
40	7sp.A	236	74	162	20	20	20	15	17	20	50	112
	B		31·3	68·7	8·5	8·5	8·5	6·3	7·2	8·5	21·2	47·5
	C				12·3	12·3	12·3	9·3	10·5	12·3	32·4	67·6
	D				17·8	17·8	17·8	13·4	15·2	17·8		
41	7sp.A	236	77	159	15	19	19	17	16	21	52	107
	B		32·7	67·3	6·4	8·0	8·0	7·2	6·8	8·9	22·0	45·3
	C				9·4	11·9	11·9	10·7	10·7	13·2	32·7	66·3
	D				14·0	17·8	17·8	15·9	14·9	19·6		
42	7sp.A	236	78	158	16	18	16	16	15	22	55	103
	B		32·9	67·1	6·8	7·6	6·8	6·8	6·4	9·3	23·4	43·7
	C				10·1	11·4	10·1	10·1	9·5	13·9	34·8	65·2
	D				15·5	17·5	15·5	15·5	14·6	21·4		
43	7sp.B	236	75	161	17	17	17	17	17	22	54	107
	B		31·8	68·2	7·2	7·2	7·2	7·2	7·2	9·3	22·9	45·3
	C				10·6	10·6	10·6	10·6	10·6	13·7	33·5	66·5
	D				15·9	15·9	15·9	15·9	15·9	20·6		
44	7sp.B	248	80	168	17	18	18	16	17	24	58	110
	B		32·3	67·7	6·8	7·3	7·3	6·4	6·8	9·7	23·4	44·3
	C				10·1	10·7	10·7	9·4	10·1	14·7	34·5	65·5
	D				15·4	16·4	16·4	14·5	15·4	21·8		
45	5sp.	262	80	182	20	20	19	18	17	24	58	110
	B		28·3	71·7	7·9	7·9	7·5	7·1	6·7	11·0	23·6	48·1
	C				11·4	11·4	10·8	10·2	9·7	15·9	34·1	65·9
	D				17·5	17·5	16·7	15·8	14·9	24·6		
46	5sp.	264	84	180	20	20	19	18	17	26	60	120
	B		31·8	68·2	7·6	7·6	7·2	6·8	6·4	9·8	22·7	45·5
	C				11·1	11·1	10·5	10·0	9·5	14·4		
	D				16·7	16·7	15·8	15·0	14·2	21·7		
47	5sp.	266	87	179	20	21	20	20	19	25	54	125
	B		31·8	68·2	7·5	7·9	7·5	7·5	7·1	9·4	20·3	46·9
	C				11·2	11·7	11·2	11·2	10·6	14·0	30·2	69·8
	D				16·0	16·8	16·0	16·0	15·2	20·0		

TABLE 15 (continued).

No.	Instar	T.L.	C.L.	A.L.	A.S1	A.S2	A.S3	A.S4	A.S5	A.S6	T	A.S1–S6
48	5sp.	284	87	197	20	25	22	20	20	28	62	135
	B		30·8	69·2	7·0	8·8	7·7	7·0	7·0	9·9	21·8	47·4
	C				10·1	12·7	11·2	10·1	10·1	14·2	31·5	68·5
	D				14·8	18·5	16·3	14·8	14·8	20·7		
49	5sp.	296	90	206	22	25	23	23	21	27	65	141
	B		30·4	69·6	7·4	8·4	7·8	7·8	7·1	9·1	22·0	47·6
	C				10·7	12·1	11·2	11·2	10·1	13·1	31·5	68·5
	D				15·6	17·7	16·3	16·3	14·9	19·1		
50	3sp.	272	90	182	20	20	19	18	17	28	60	122
	B		33·3	66·7	7·3	7·3	7·0	6·6	6·2	10·2	22·1	44·6
	C				11·0	11·0	10·4	9·9	9·3	15·3	33·0	66·0
	D				16·4	16·4	15·6	14·7	13·9	22·9		
51	3sp.	276	90	186	21	21	18	18	18	27	63	123
	B		32·6	67·4	7·6	7·6	6·5	6·5	6·5	9·0	22·8	44·6
	C				11·3	11·3	9·7	9·7	9·7	14·5	33·9	66·2
	D				17·1	17·1	14·6	14·6	14·6	22·0		
52	3sp.	282	93	189	21	21	21	21	18	27	60	129
	B		33·0	67·0	7·4	7·4	7·4	7·4	6·4	9·6	21·3	45·7
	C				11·1	11·1	11·1	11·1	9·5	14·3	31·8	68·3
	D				16·3	16·3	16·3	16·3	14·0	20·9		
53	3sp.	285	90	195	21	21	21	21	18	27	66	129
	B		31·6	68·4	7·4	7·4	7·4	7·4	6·3	9·5	23·2	45·3
	C				10·8	10·8	10·8	10·8	14·0	11·0	33·8	66·2
	D				16·3	16·3	16·3	16·3	14·0	21·0		
54	3sp.	288	90	198	21	21	21	21	18	27	69	129
	B		31·2	68·8	7·3	7·3	7·3	7·3	6·3	9·4	24·0	44·8
	C				10·6	10·6	10·6	10·6	9·1	13·6	34·8	65·2
	D				16·3	16·3	16·3	16·3	14·0	20·9		
55	3sp.	296	85	213	27	24	24	24	24	30	60	153
	B		28·1	71·9	9·1	8·1	8·1	8·1	8·1	10·1	20·3	51·6
	C				12·7	11·3	11·3	11·3	11·3	14·1	28·2	71·8
	D				17·6	15·7	15·7	15·7	15·7	19·6		
56	1sp.3PL	294	90	204	24	24	24	21	21	27	63	141
	B		30·6	69·4	8·2	8·2	8·2	7·1	7·1	9·2	21·4	48·0
	C				11·8	11·8	11·8	10·3	10·3	13·2	30·9	69·1
	D				17·0	17·0	17·0	14·9	14·9	19·1		
57	1sp.3PL	316	94	222	23	25	25	25	24	30	70	152
	B		29·8	70·2	7·3	7·9	7·9	7·9	7·9	9·5	22·2	48·0
	C				10·4	11·3	11·3	11·3	10·8	13·5	31·6	68·5
	D				15·1	16·4	16·4	16·4	15·8	19·7		
58	1sp.3PL	318	96	222	27	24	24	24	21	27	75	147
	B		30·2	69·8	8·5	7·5	7·5	7·5	6·6	8·5	23·6	46·2
	C				12·2	10·8	10·8	10·8	9·5	12·2	33·8	66·2
	D				18·5	16·3	16·3	16·3	14·3	18·4		
59	1sp.3PL	328	97	231	30	27	24	27	27	30	66	165
	B		29·8	70·2	9·1	8·2	7·3	8·2	8·2	9·1	20·1	50·1
	C				13·0	11·7	10·4	11·7	11·7	13·0	28·6	71·4
	D				18·2	16·4	14·5	16·4	16·4	18·2		
60	1sp.3PL	341	101	240	33	30	27	27	27	30	66	174
	B		29·7	70·3	9·7	8·8	7·9	7·9	7·9	8·8	19·3	51·0
	C				13·7	12·5	11·2	11·2	11·2	12·5	27·5	72·5
	D				19·0	17·2	15·5	15·5	15·5	17·2		
61	1sp.3PL	372	120	252	30	27	27	27	27	33	81	171
	B		32·2	67·8	8·1	7·3	7·3	7·3	7·3	8·9	21·8	46·0
	C				11·9	10·7	10·7	10·7	10·7	13·1	32·2	67·8
	D				17·5	15·8	15·8	15·8	15·8	19·2		
62	1sp.2PL	362	96	266	36	33	30	30	30	36	72	195
	B		26·6	73·4	9·9	9·1	8·3	8·3	8·3	9·9	19·6	53·8
	C				13·5	12·4	11·3	11·3	11·3	13·5	26·7	73·3
	D				18·5	16·9	15·4	15·4	15·4	18·5		
63	1sp.2PL	374	109	265	30	32	32	32	31	36	72	193
	B		29·1	70·9	8·0	8·6	8·6	8·6	8·3	9·6	9·2	51·7
	C				11·3	12·1	12·1	12·1	11·7	13·6	27·2	72·8
	D				15·5	16·6	16·6	16·6	16·1	18·6		

TABLE 15 (continued).

No.	Instar	T.L.	C.L.	A.L.	A.S1	A.S2	A.S3	A.S4	A.S5	A.S6	T	A.S1–S6
64	1sp.2PL	392	114	278	39	36	33	30	30	36	74	204
	B		29·3	70·7	9·9	9·2	8·4	7·6	7·6	9·2	18·8	51·9
	C				14·0	12·9	11·9	10·8	10·8	12·9	26·2	73·8
	D				19·1	17·6	16·2	14·7	14·7	17·6		
65	1sp.2PL	412	120	282	39	38	34	31	31	37	74	210
	B		31·5	68·5	9·5	9·2	8·3	7·5	7·5	9·0	17·9	51·0
	C				13·8	13·5	12·1	11·0	11·0	13·1	26·2	73·8
	D				18·6	18·1	16·2	14·8	14·8	17·6		
66	1sp.2PL	421	106	295	35	35	33	34	34	38	86	209
	B		30·0	7·0	8·3	8·3	7·8	8·1	8·1	9·0	20·4	49·7
	C				11·9	11·9	11·1	11·5	11·5	12·9	29·2	70·8
	D				16·7	16·7	15·8	16·3	16·3	18·2		
67	♀	438	126	312	42	39	36	36	36	42	84	228
	B		28·8	71·2	9·6	8·9	8·2	8·2	7·5	9·6	19·2	52·0
	C				13·5	12·5	11·6	11·6	10·6	13·5	27·0	73·0
	D				18·4	17·1	15·8	15·8	14·5	18·4		
68	♂	461	135	326	42	39	39	39	36	48	83	243
	B		29·2	70·8	9·1	8·5	8·5	8·5	7·8	10·4	18·0	52·8
	C				12·9	12·0	12·0	12·0	11·0	14·7	25·5	74·5
	D				17·3	16·0	16·0	16·0	14·8	19·7		
69	♂	468	144	324	39	39	36	36	36	48	90	234
	B		30·8	69·2	8·3	8·3	7·7	7·7	7·7	10·3	19·2	50·0
	C				12·0	12·0	11·1	11·1	11·1	14·8	27·8	72·2
	D				16·7	16·7	15·4	15·4	15·4	20·5		
70	♀	474	144	330	45	39	39	39	39	45	84	246
	B		30·3	69·7	9·5	8·2	8·2	8·2	8·2	9·5	17·7	52·0
	C				13·6	11·8	11·8	11·8	11·8	13·6	25·5	74·5
	D				18·3	15·8	15·8	15·8	15·8	18·3		
71	♀	492	150	342	45	45	42	42	45	45	78	264
	B		30·5	69·5	9·1	9·1	8·5	8·5	9·1	9·1	15·8	53·7
	C				13·2	13·2	12·3	12·3	13·2	13·2	22·8	77·2
	D				17·1	17·1	15·9	15·9	17·1	17·1		
72	♀	498	156	342	42	42	42	42	42	45	87	255
	B		31·3	68·7	8·4	8·4	8·4	8·4	8·4	9·0	17·5	51·2
	C				12·3	12·3	12·3	12·3	12·3	13·2	25·4	74·6
	D				16·5	16·5	16·5	16·5	16·5	17·7		
73	♂	510	156	354	45	45	45	42	39	45	93	261
	B		30·6	69·4	8·8	8·8	8·8	8·2	7·6	8·5	18·2	51·2
	C				12·7	12·7	12·7	11·9	11·1	12·7	26·1	73·9
	D				17·2	17·2	17·2	16·1	14·9	17·3		
74	♂	516	162	354	45	45	45	42	39	45	93	261
	B		31·4	68·6	8·7	8·7	8·7	8·1	7·6	8·7	18·0	50·6
	C				12·7	12·7	12·7	11·9	11·0	12·7	26·3	73·7
	D				17·2	17·2	17·2	16·1	14·9	17·3		
75	♂	520	158	362	45	45	45	45	45	48	89	273
	B		29·6	70·4	8·6	8·6	8·6	8·6	8·6	9·3	18·1	52·3
	C				12·4	12·4	12·4	12·4	12·4	13·3	24·6	75·4
	D				16·5	16·5	16·5	16·5	16·5	17·6		
76	♀	528	156	372	51	45	45	42	45	48	96	276
	B		31·0	69·0	9·7	8·5	8·5	7·9	8·5	8·1	18·2	50·8
	C				13·7	12·1	12·1	11·3	12·1	12·9	25·8	74·2
	D				18·5	16·3	16·3	15·2	16·3	17·4		
77	♀	534	168	366	48	45	42	42	45	48	96	270
	B		31·4	68·6	9·0	8·4	7·9	7·9	8·4	9·0	18·0	50·6
	C				13·1	12·3	11·5	11·5	12·3	13·1	26·2	73·8
	D				17·8	16·7	15·6	15·6	16·7	17·8		
78	♂	540	159	381	48	48	45	45	45	51	99	282
	B		29·5	70·5	8·9	8·9	8·3	8·3	8·3	9·5	18·3	52·2
	C				12·6	12·6	11·8	11·8	11·8	13·4	26·0	74·0
	D				17·0	17·0	16·0	16·0	16·0	18·0		
79	♂	563	171	392	48	48	45	48	48	54	101	291
	B		30·5	69·5	8·5	8·5	8·0	8·5	8·5	9·6	17·9	51·6
	C				12·2	12·2	11·5	12·2	12·2	13·8	25·8	74·2
	D				16·5	16·5	15·5	16·5	16·5	18·6		

TABLE 15 (continued).

No.	Instar	T.L.	C.L.	A.L.	A.S1	A.S2	A.S3	A.S4	A.S5	A.S6	T	A.S1–S6
80	♀	570	186	384	45	45	45	45	45	54	105	279
	B		32·6	67·4	7·9	7·9	7·9	7·9	7·9	9·5	18·4	49·0
	C				11·7	11·7	11·7	11·7	11·7	14·1	27·4	72·6
	D				16·1	16·1	16·1	16·1	16·1	19·4		
81	♀	582	186	396	54	48	48	48	48	48	102	294
	B		32·0	68·0	9·3	8·2	8·2	8·2	8·2	8·2	17·5	50·5
	C				13·6	12·1	12·1	12·1	12·1	12·1	25·8	74·2
	D				18·4	16·3	16·3	16·3	16·3	16·3		
82	♂	594	186	408	52	50	48	48	48	54	108	300
	B		31·3	68·7	8·7	8·1	8·1	8·1	8·1	9·1	18·2	50·5
	C				12·8	12·3	11·8	11·8	11·8	13·3	26·5	73·5
	D				17·3	16·7	16·0	16·0	16·0	18·0		
83	♂	604	166	438	56	53	50	56	53	60	110	328
	B		27·5	72·5	9·3	8·7	8·3	8·3	8·7	9·9	18·2	54·3
	C				12·8	12·1	11·4	12·8	12·1	13·7	25·1	74·9
	D				17·1	16·2	15·2	17·1	16·2	18·3		
84	♂	612	192	420	51	48	48	48	48	54	123	297
	B		31·4	68·6	8·3	7·8	7·8	7·8	7·8	8·8	20·3	48·3
	C				12·2	11·4	11·4	11·4	11·4	12·9	29·3	70·7
	D				17·2	16·2	16·2	16·2	16·2	18·1		
85	♂	618	198	420	51	48	48	48	51	54	120	300
	B		29·8	70·2	8·2	7·8	7·8	7·8	8·2	8·7	19·4	48·6
	C				12·2	11·4	11·4	11·4	12·2	12·9	28·5	71·5
	D				17·0	16·0	16·0	16·0	17·0	18·0		
86	♂	624	186	438	51	48	48	48	48	47	147	291
	B		32·0	68·0	8·2	7·7	7·7	7·7	7·7	7·7	23·6	46·6
	C				11·7	11·0	11·0	11·0	11·0	11·0	33·5	66·5
	D				17·5	16·5	16·5	16·5	16·5	16·5		
87	♀	630	210	420	60	57	54	51	51	51	96	324
	B		33·4	66·5	9·5	9·0	8·6	8·1	8·1	8·1	15·0	51·5
	C				14·3	13·6	12·9	12·1	12·1	12·1	22·0	67·1
	D				18·5	17·6	16·7	15·7	15·7	15·7		
88	♂	542	204	438	54	54	54	54	54	60	108	330
	B		31·8	68·2	8·4	8·4	8·4	8·4	8·4	9·3	16·8	51·5
	C				12·3	12·3	12·3	12·3	12·3	13·7	24·6	75·4
	D				16·4	16·4	16·4	16·4	16·4	18·2		
89	♀	648	222	426	57	54	51	54	54	54	102	324
	B		34·3	65·7	8·8	8·3	7·9	8·3	8·3	8·3	15·7	50·0
	C				13·4	12·7	12·0	12·7	12·7	12·7	24·0	76·0
	D				17·6	16·7	15·7	16·7	16·7	16·7		
90	♂	672	222	450	60	57	54	54	51	57	117	333
	B		33·0	67·0	8·9	8·5	8·0	8·0	7·6	8·5	17·4	49·6
	C				13·3	12·7	12·0	12·0	11·3	12·7	26·0	74·0
	D				18·0	17·1	16·2	16·2	15·3	17·1		
91	♂	708	228	480	63	60	57	57	57	63	123	357
	B		32·2	67·8	8·9	8·5	8·1	8·1	8·1	8·9	17·4	50·4
	C				13·1	12·5	11·9	11·9	11·9	13·1	25·5	74·4
	D				17·6	16·8	16·0	16·0	16·0	16·8		
92	♀	714	234	480	66	60	54	54	57	60	129	351
	B		32·8	67·2	9·2	8·4	7·5	7·5	8·0	8·4	18·1	49·1
	C				13·7	12·5	11·3	11·3	11·9	12·5	26·7	73·3
	D				18·8	17·1	15·4	15·4	16·2	17·1		
93	♀	724	248	476	66	56	50	60	60	66	118	358
	B		34·0	66·0	9·1	7·7	6·9	8·3	8·3	9·1	16·6	49·4
	C				13·9	11·8	10·5	12·6	12·6	13·9	24·8	75·2
	D				18·4	15·6	14·0	16·8	16·8	18·4		
94	♀	726	240	486	60	60	60	57	57	60	132	354
	B		33·1	66·9	8·3	8·3	8·3	7·8	7·8	8·3	18·2	48 7
	C				12·3	12·3	12·3	11·7	11·7	12·3	27·2	72·8
	D				17·0	17·0	17·0	16·1	16·1	17·0		
95	♀	726	252	474	60	57	57	57	57	60	126	348
	B		34·7	65·3	8·3	7·8	7·8	7·8	7·8	8·3	17·4	47·9
	C											

TABLE 15 (continued).

No.	Instar	T.L.	C.L.	A.L.	A.S1	A.S2	A.S3	A.S4	A.S5	A.S6	T	A.S1–S6
96	♀	768	264	504	69	60	57	60	63	66	129	375
	B		34·4	65·6	9·0	7·8	7·4	7·8	8·2	8·5	16·8	48·8
	C				13·7	11·9	11·3	11·9	12·5	13·1	15·6	74·6
	D				18·4	16·0	15·2	16·0	16·8	17·6		
97	♀	780	264	516	75	66	63	63	60	63	126	390
	B		33·8	66·2	9·6	8·5	8·1	8·1	7·7	8·1	16·2	50·0
	C				14·5	12·8	12·2	12·2	11·6	12·2	24·4	75·6
	D				19·2	16·9	16·2	16·2	15·4	16·2		
98	♀	784	238	546	71	66	66	71	71	71	130	416
	B		30·2	69·8	9·1	8·4	8·4	9·1	9·1	9·1	16·6	53·2
	C				13·0	12·1	12·1	13·0	13·0	13·0	23·8	76·2
	D				17·1	15·9	15·9	17·1	17·1	17·1		
99	♀	804	270	534	75	66	66	66	63	69	129	405
	B		33·6	66·4	9·3	8·2	8·2	8·2	7·8	8·6	16·0	50·4
	C				14·1	12·4	12·4	12·4	11·8	12·9	24·2	75·8
	D				18·5	16·3	16·3	16·3	15·5	17·0		
100	♀	810	270	540	72	69	66	63	66	72	132	408
	B		33·4	66·6	8·9	8·5	8·1	7·8	8·1	8·9	16·3	50·3
	C				13·3	12·8	12·2	11·7	12·2	13·3	24·5	75·5
	D				17·7	16·9	16·2	15·4	16·2	17·7		
101	♀	816	288	528	72	69	63	63	66	69	126	402
	B		35·3	64·7	8·8	8·4	7·7	7·7	8·1	8·4	15·4	49·3
	C				13·6	13·1	11·9	11·9	12·5	13·1	23·9	76·1
	D				17·9	17·1	15·7	15·7	16·4	17·1		
102	♂	846	270	576	76	69	69	69	69	69	156	420
	B		31·9	68·1	8·9	8·0	8·0	8·0	8·0	8·0	18·4	49·7
	C				13·0	12·0	12·0	12·0	12·0	12·0	27·1	72·9
	D				17·9	16·4	16·4	16·4	16·4	16·4		
103	♀	846	288	558	72	72	63	66	72	75	135	423
	B		34·1	65·9	8·9	8·5	7·4	7·8	8·5	8·9	15·9	50·0
	C				13·4	12·9	11·3	11·8	12·9	13·4	24·2	75·8
	D				17·7	17·0	14·9	15·6	17·0	17·7		
104	♀	870	300	570	72	72	72	72	72	75	135	435
	B		34·5	65·5	8·3	8·3	8·3	8·3	8·3	8·6	15·5	50·0
	C				12·6	12·6	12·6	12·6	12·6	13·2	23·6	76·4
	D				16·6	16·6	16·6	16·6	16·6	17·2		
105	♀	876	294	582	78	75	75	72	72	75	135	447
	B		33·6	66·4	8·9	8·6	8·6	8·2	8·2	8·6	15·4	51·0
	C				13·4	12·9	12·9	12·4	12·4	12·9	23·2	76·8
	D				17·5	16·8	16·8	16·1	16·1	17·5		
106	♀	882	300	582	78	72	72	72	72	78	138	444
	B		34·1	65·9	8·8	8·1	8·1	8·1	8·1	8·8	15·6	50·3
	C				13·4	12·4	12·4	12·4	12·4	13·4	23·7	76·3
	D				17·6	16·2	16·2	16·2	16·2	17·6		
107	♂	888	288	600	80	75	75	75	75	75	135	465
	B		32·5	67·5	10·1	8·4	8·4	8·4	8·4	8·4	15·2	52·3
	C				15·0	12·5	12·5	12·5	12·5	12·5	22·5	77·5
	D				19·3	16·1	16·1	16·1	16·1	16·1		
108	♀	900	300	600	78	75	75	75	72	75	150	450
	B		33·3	66·7	8·7	8·3	8·3	8·3	8·0	8·3	16·7	50·0
	C				13·0	12·5	12·5	12·5	12·0	12·5	25·0	75·0
	D				17·3	16·7	16·7	16 7	16·0	16·7		
109	♀	918	318	600	78	75	69	69	69	81	159	441
	B		34·7	65·3	8·5	8·2	7·5	7·5	7·5	8·8	17·3	48·0
	C				13·0	12·5	11·5	11·5	11·5	13·5	26·5	73·5
	D				17·7	17·0	15·6	15·6	15·6	18·4		
110	♀	924	306	618	84	78	75	75	75	81	144	474
	B		33·1	66·9	9·1	8·4	8·1	8·1	8·1	8·7	15·6	51·3
	C				13·6	12·6	12·1	12·1	12·1	13·1	23·3	76·7
	D				17·7	16·4	15·8	15·8	15·8	17·1		

TABLE 15 (continued).

No.	Instar	T.L.	C.L.	A.L.	A.S1	A.S2	A.S3	A.S4	A.S5	A.S6	T	A.S1–S6
111	♂	954	300	654	90	90	81	78	78	87	150	504
	B		31·4	68·6	9·4	9·4	8·5	8·5	8·5	9·1	15·7	52·9
	C				13·8	13·8	12·4	12·4	12·4	13·3	22·9	77·1
	D				17·9	17·9	16·0	15·4	15·4	17·3		
112	♂	960	300	660	96	78	78	78	78	84	168	492
	B		31·2	68·8	10·0	8·1	8·1	8·1	8·1	8·7	17·5	51·3
	C				14·5	11·8	11·8	11·8	11·8	12·7	25·4	74·6
	D				19·5	15·8	15·8	15·8	15·8	17·1		
113	♀	960	315	645	93	84	78	78	78	78	156	489
	B		32·8	67·2	9·7	9·7	8·1	8·1	8·1	8·1	16·2	51·0
	C				14·4	13·0	12·1	12·1	12·1	12·1	24·2	75·8
	D				19·0	17·0	16·0	16·0	16·0	16·6		
114	♀	966	330	636	90	78	78	78	78	78	156	480
	B		34·2	65·8	9·3	8·1	8·1	8·1	8·1	8·1	16·1	49·7
	C				14·2	12·3	12·3	12·3	12·3	12·3	24·5	75·5
	D				18·7	16·2	16·2	16·2	16·2	16·2		
115	♂	966	300	666	90	84	84	84	84	84	156	510
	B		31·1	68·9	9·3	8·7	8·7	8·7	8·7	8·7	16·1	52·8
	C				13·5	12·6	12·6	12·6	12·6	12·6	23·4	76·6
	D				17·7	16·5	16·5	16·5	16·5	16·5		
116	♀	990	336	654	90	78	78	84	84	84	156	498
	B		33·9	66·1	9·1	7·9	7·9	8·5	8·5	8·5	15·8	50·3
	C				13·8	11·9	11·9	12·9	12·9	12·9	23·9	76·1
	D				18·1	15·7	15·7	16·9	16·9	16·9	16·9	
117	♀	1032	348	684	90	90	90	90	84	90	150	534
	B		33·7	66·3	8·7	8·7	8·7	8·7	8·1	8·7	14·7	51·6
	C				13·2	13·2	13·2	13·2	12·3	13·2	22·0	78·0
	D				16·8	16·8	16·8	16·8	15·7	16·8		
118	♂	1062	330	732	96	96	90	96	96	96	162	570
	B		31·1	68·9	9·0	9·0	8·5	9·0	9·0	9·0	15·3	53·6
	C				13·1	13·1	12·3	13·1	13·1	13·1	22·2	77·8
	D				16·8	16·8	15·8	16·8	16·8	16·8		
119	♀	1086	384	702	90	90	90	90	90	90	162	540
	B		35·4	64·6	8·3	8·3	8·3	8·3	8·3	8·3	14·9	49·7
	C				12·8	12·8	12·8	12·8	12·8	12·8	23·1	76·9
	D				16·7	16·7	16·7	16·7	16·7	16·7		
120	♂	1170	360	810	180	108	99	105	108	108	174	636
	B		30·8	69·2	9·2	9·2	8·5	9·0	9·2	9·2	14·9	54·3
	C				13·3	13·3	12·2	13·0	13·3	13·3	21·5	78·5
	D				17·0	17·0	15·5	16·5	17·0	17·0		
121	♂	1176	360	816	111	108	102	105	108	108	174	642
			30·6	69·4	9·4	9·2	8·7	8·9	9·2	9·2	14·8	54·6
	D				13·6	13·2	12·5	12·9	13·2	13·2	21·5	78·5
					17·3	16·8	15·9	16·4	16·8	16·8		

I. Bibliography.

1. Biology.

Banner, A. H., 1950. A taxonomic study of the Mysidacea and Euphausiacea (Crustacea) of the North Eastern Pacific. III Euphausiacea. Trans. Roy. Canad. Inst. V. 29, 1-62.

Bargmann, H. E., 1937. The reproductive system of *Euphausia superba*. Discovery Reports V. 14, 325-350.

Bargmann, H. E., 1945. The development and life-history of adolescent and adult Krill, *Euphausia superba*. Discovery Reports V. 23, 103-176.

Bigelow, H. B., 1924. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bur. Fish. V. 40, pt. 2 (133-156).

Boden, B. P., 1950. The post-naupliar stages of the crustacean *Euphausia pacifica*. Trans. Am. Micr. Soc. V. 69, No. 4, 373-386.

Boden, B. P., 1951. The egg and larval stages of *Nyctiphanes simplex*, a Euphausiid crustacean from California. Proc. Zool. Soc., Lond. V. 121, pt. 3, 515-527.

Boone, L., 1935. Crustacea. Sci. Res. "Alva" 1931. Bull. Vanderbilt mar. mus. V. 6, 204-211.

Brook, G., and Hoyle, W. E., 1888. The metamorphosis of British Euphausiidae. Proc. Roy. Soc. Edinb. V. 15.

California Co-operative Sardine Research Programme, 1950. Progr. Rep. 1950 State of California, Dept. Nat. Res. Mar. Res. Committee, 35.

Calman, W. T., 1896. On deep-sea Crustacea from the south-west coast of Ireland. Trans. R. Irish Acad. V. 31, pt. 1, 1-22.

Calman, W. T., 1905. Note on a genus of Euphausiid Crustacea. Fisheries Ireland Sci. Invest. 1902-03, V. 4, 153-155.

Coe, W. R., 1946. The means of dispersal of bathypelagic animals in the North and South Atlantic. Amer. Nat. V. 80, 453-469.

*Colosi, G., 1916. Contributo alla conoscenza degli Schizopodi dello stretto di Messina. Monit. Zool. Ital., V. 27, 61-64.

*Colosi, G., 1917a. Eufausiacei raccolti nel Mediterrano dalla R. Nave Washington. Bull. Soc. Entomol. Ital. V. 48, 118-130.

*Colosi, G., 1917b. Raccolte planchtoniche "Liguria," Crostacei—Parte II. Eufausiacei R. 1st di studi, superiori practici e di perfzeionamento V. 2, Fasc. 7, 165-205.

*Colosi, G., 1918. Sul genere *Meganyctiphanes* (Eufausiacei). Monit. Zool. Italiano V. 29, N. 11, p. 12.

*Colosi, G., 1922. Eufausiacei e Mysidacei dello Stretto di Messina. R. Comit Tallassogr. Ital. Mem. 98.

Dakin, W. J., and Colefax, A. N., 1940. The plankton of the Australian coastal waters of New South Wales 1. Publ. Uni. Sydney, Dept. Zool. Monogr. No. 1, 1-215.

Deacon, G. E. R., 1937. The Hydrology of the Southern Ocean. Discovery Reports V. 15, 3-124.

Einarsson, H., 1942. Notes on Euphausiacea, 1-111. Vidensk. Medd. fra Dansk. Naturk. V. 106, 263-286.

Einarsson, H., 1945. Euphausiacea, 1. North Atlantic species. Dana Report No. 27, 1-185.

Esterly, C. O., 1914. The vertical distribution and movements of the Schizopoda of the San Diego Region. Univ. Cal. Publn. Zool. V. 13, No. 5, 123-145.

Fraser, J. H., 1936. On the development and distribution of the Krill *(Euphausia superba)*. Discovery Reports V. 14, 1-192.

Frost, W. E., 1932. Observations on the reproduction of *Nyctiphanes couchii* (Bell) and *Meganyctiphanes norvegica* (Sars) off the south coast of Ireland. Proc. Roy. Soc. Irish Acad. V. XL, Sect. B, No. 14, 194-232.

Frost, W. E., 1934. The occurrence and development of *Euphausia krohnii* off the south-west coast of Ireland. *Ibid.*, V. XLII, Sect. B, No. 3, 17-46.

Frost, W. E., 1935. Larval Stages of the Euphausiids *Nematoscelis megalops* (G.O.S.) and *Stylocheiron longicorne* (G.O.S.) taken off the south-west coast of Ireland. *Ibid.*, V. XLII, Sect. B, No. 16, 443-458.

Frost, W. E., 1939. Larval Stages of the Euphausiid *Thysanopoda acutifrons* (Holt and Tattersall) taken off the south-west coast of Ireland. *Ibid.*, V. XLV, Sect. B., No. 13, 301-319.

Gurney, R., 1942. Larvae of Decapod Crustacea. Ray Society, London.

Gurney, R., 1947. Notes on the development of the Euphausiacea. Proc. Zool. Soc. Lond., 49-64.

Hansen, H. J., 1905a. Preliminary report on the Schizopoda of the Cruise of the "Princesse-Alice" in the year 1904. Bull. Mus. Oceanogr. de Monaco No. 30, 1-32.

Hansen, H. J., 1905b. Further notes on the Schizopoda. *Ibid.*, No. 42, 1-32.

Hansen, H. J., 1908a. Crustacea Malacostracea I. The Danish Ingolf Exp. V. 3, Pt. 2, 1-120.

Hansen, H. J., 1908b. Schizopoda and Cumacea—Exp. Antarctique Belge. Resultats du Voyage du S. Y. Belgica en 1897-1898-1899. Rapp. Scient. Zool. Anvers, 1-7.

Hansen, H. J., 1910. The Schizopoda of the Siboga Expedition. Siboga-Expeditie XXXVII, 1-123.

Hansen, H. J., 1911. The Genera and Species of the Order Euphausiacea with an account of a remarkable variation. Bull. Inst. Oceanogr. Monaco, No. 210, 1-54.

Hansen, H. J., 1912. The Schizopoda. Rep. "Albatross" Exp. Mem. Mus. Comp. Zool. Harv. V. XXXV, No. 4, 175-296.

Hansen, H. J., 1913. Crustacea Schizopoda. Rept. Swed. Antarct. Expd. 1901-03, 1-56.

Hansen, H. J., 1915. The Crustacea Euphausiacea of the United States National Museum. Proc. of the U.S. Nat. Mus. V. 48, 1-56.

Hansen, H. J., 1916. The Euphausiacean Crustaceans of the "Albatross" Expedition to the Philippines. Proc. U.S. Nat. Mus. V. 49, 635-654.

Hardy, A. C., 1924. The Herring in Relation to its Animate Environment, Part I. The food and feeding habits of the Herring, with special reference to the east coast of England. Fish. Invest. Ser. 2, V. 7, No. 3.

Hardy, A. C., 1936. Observations in the uneven distribution of the oceanic plankton. Discovery Reports V. 11, 511-538.

Hardy, A. C., and Gunther, E. R., 1935. The plankton of South Georgia whaling grounds and adjacent waters. Discovery Reports V. 7, 1-377.

Hardy, A. C., and Paton, W. H., 1947. Vertical migration of plankton animals. Journ. Mar. Biol. Ass. U.K. V. 26, 467-523.

Hardy, A. C., and Bainbridge, R., 1951. Vertical migration of plankton animals. Nature V. 168, 4269, 327-328.

Hickling, C. F., 1925. Notes on Euphausiids. Journ. Mar. Biol. Assoc. V. XIII, No. 3, 735-745.

Holt, E. W. L., and Tattersall, W. M., 1905. Schizopodous Crustacea from the North-east Atlantic Slope. Ann. Rep. Fish. Ireland, 1902-03. Part 2, appen. 4, 99-152.

Illig, G., 1930. Die Schizopoden de Deutschen Tief-see Expedn. 1898-1899. Deutsch. Tiefsee. Expd. 1898-99, "Valdivia" V. 22, pt. 6, 400-625.

Jespersen, P., 1940. Investigations on the quantity and distribution of marine organisms in Icelandic Waters. Medd. Kom. Dan. Fisk. Havind Ser. Plankton V. 3, 1-77.

John, D. D., 1936. The Southern Species of the genus *Euphausia*. Discovery Reports V. 14, 193-325.

Ketchum, B. H., 1947. The biochemical relations between marine organisms and their environment. Woods Hole Oceanor. Inst., Contrib. 377 (Ecol. Monogr. V. 17, 1947, 309-315).

Lebour, M. V., 1924. The Euphausiidae in the Neighbourhood of Plymouth and their Importance as Herring Food. Journ. Mar. Biol. Assoc. V. 13, No. 2, 402-432.

Lebour, M. V., 1925. The Euphausiidae in the Neighbourhood of Plymouth II. *Nyctiphanes couchii* and *Meganyctiphanes norvegica*. *Ibid.*, V. 13, No. 4, 810-828.

Lebour, M. V., 1926a. The Euphausiidae in the Neighbourhood of Plymouth III. *Thysanoessa inermis*. *Ibid.*, V. 14, No. 1, 1-21.

Lebour, M. V., 1926b. The young of *Stylocheiron suhmii* G.O.S. and *Stylocheiron abbreviatum* G.O.S. from Mediterranean plankton, Alexandria, Egypt. Proc. Zool. Soc. London, Pt. 1, 206-211.

Lebour, M. V., 1926c. On some larval Euphausiids from the Mediterranean, Alexandria, Egypt. *Ibid.*, Pt. 3, 765-776.

Lebour, M. V., 1926d. A general survey of larval Euphausiids, with a scheme for their identification. Journ. Mar. Biol. Assoc. V. 14, No. 2, 519-527.

Lebour, M. V., 1949. Some Euphausiids from Bermuda. Proc. Zool. Soc. Lond. V. 119, 823-837.

MacDonald, R., 1926. Numerical Reduction of Instars in the Metamorphosis of Euphausiids. Nature V. 117, No. 2956, 894.

MacDonald, R., 1927a. Irregular Development in the Larval History of *Meganyctiphanes norvegica*. Journ. Mar. Biol. Assoc. V. 14, No. 3, 785-794.

MacDonald, R., 1927b. Food and Habits of *Meganyctiphanes norvegica*. *Ibid.*, V. 14, No. 3, 753-781.

MacDonald, R., 1928. The Life History of *Thysanoessa raschii*. *Ibid.*, V. 15, 57-65.

Mackintosh, N. A., 1934. Distribution of the Macroplankton in the Atlantic Sector of the Antarctic. Discovery Reports V. 9, 67-168.

Marshall, N. B., 1948. Zooplankton (other than copepods and young fish) in the North Sea, 1938-1939. Hull Bull. Mar. Ecol. Vol. 2, No. 13, 173-213.

Milne-Edwards, H., 1830. Memoire sur une disposition particuliére de l' appareil branchial de quelques Crustacées. Ann. de Sci. Nat. V. 19, 451-460.

Moore, H. B., 1950. The relation between the scattering layer and the Euphausiacea. Woods Hole Oceanogr. Inst. Contr. 535, 181-212.

Orton, J. H., 1920. Sea-temperature, Breeding and Distribution of Marine Animals. Journ. Mar. Biol. Assoc. V. 13.

Russell, F. S., 1927. The vertical distribution of plankton in the sea. Biol. Rev. V. 2, No. 3, 213-262.

Rustad, D., 1930. Euphausiacea, with notes on their biogeography and development. Sci. Res. Norw. Antarctic Exp. 1927-28, and 1928-29 No. 5, Dept. norske Vid. Akad i Oslo, 1-83.

Rustad, D., 1934. On the antarctic Euphausiids from the "Norvegica" Exp. 1929-30 and 1930-31. *Ibid.*, No. 12, 1-53.

Ruud, J. T., 1927. Zooplankton off the coast of More, 1926. A. Euphausiidae Rep. of the Area Comm. North-eastern Area Appendix A. Rapp. et Proc. Verb. des Reunions. V. 41.

Ruud, J. T., 1928. Fluctuations in the larval stages of Euphausiidae, off More, 1926-27. Journ. d. Conseil. V. 3, 1, 98-101.

Ruud, J. T., 1932. On the Biology of Southern Euphausiidae. Hvalradets Skrifter Nr. 2 Oslo, 5-105.

Ruud, J. T., 1936. Euphausiacea. Rep. Danish Oceanogr. Exp. 1908-10 to Medit. and Adj. Seas II, D.6.

Sars, G. O., 1885. Report on the Schizopoda. Challenger Reports. Zool. V. 13, 1-288.

Sars, G. O., 1889. On the propagation and early development of Euphausiidae. Arch. Math. Naturv. 20.

Schmitt, W. L., 1919. The Schizopoda (Crustaceans) of the Canadian Arctic Expedition, 1913-18. Rep. of the Canad. Arctic Exp. 1913-18 V. VII, part B.

Sheard, K., 1941. Improved methods of collecting marine organisms. Rec. Sth. Austr. Mus. V. 7, No. 1, 11-14.

Sheard, K., 1942. The genus *Thysanopoda* (Crustacea Euphausiacea). Trans. R. Soc. Sth. Austr. V. 66, pt. 1, 60-65.

Sheard, K., 1947. Plankton of the Australian-Antarctic Quadrant. (1) Net-plankton volume. B.A.N.Z.A.R.E. Repts. V. 6, pt. 1, 1-19.

Sheard, K., 1949. Plankton characteristics at Cronulla, New South Wales. Comm. Sci. Ind. Res. Org. Austr. Bull. 246, 1-23.

Sheard, K., 1950. Factors in the behaviour of pelagic fish shoals in South Australia and New South Wales. pp. 72-74 in Blackburn, M., and Tubb, J. A., 1950. Measures of abundance of pelagic fish. Comm. Sci. Ind. Res. Org. Austr. Bull. 251.

Stebbing, T. R., 1900. Crustaceans of the Falkland Is. Proc. Roy. Soc. Lond., 545-546.

Sverdrup, H. V., Johnson, M. W., and Fleming, R. H., 1946. The Oceans, their Physics, Chemistry and General Biology. New York, Prentice Hall, Inc., 1-1087.

Tattersall, W. M., 1924. Euphausiacea. British Antarctic, "Terra Nova" Exp. 1910. Nat. Hist. Rep. Zool. V. 13, No. 1, Crustacea Pt. VIII, 1-36.

Tattersall, W. M., 1925. Mysidacea and Euphausiacea of Marine Survey, South Africa, Union of S. Africa. Fisheries and Mar. Biol. Survey Rep. No. 4 for the year 1924, 1-12.

Tattersall, W. M., 1926. Crustacea of the Order Euphausiacea and Mysidacea from the Western Atlantic. Proc. U.S. Nat. Mus. V. 69, Art. 8, 1-31.

Tattersall, W. M., 1933. Euphausiacea and Mysidacea from Western Canada. Contrib. to Canad. Biol. and Fisheries V. VIII, No. 15, 1-25.

Tattersall, W. M., 1936. Mysidacea and Euphausiacea. Great Barrier Reef Exp. (1928-29) Sci. Rep. V. 4, 143-176.

Tattersall, W. M., 1939. The Euphausiacea and Mysidacea of the John Murray Exp. to the Indian Ocean. The John Murray Exp. (1933-34) Sci. Rep. V. V, No. 8, 203-246.

*Torelli, B., 1934. Euphausacei. R. Comm. Talassogr. Hal. No. 208.

Wimpenny, R. S., 1937. The Distribution, Breeding and Feeding of some important Plankton Organisms of the South-west North Sea in 1934. Fishery Invest. Ser. II, V. XV, No. 3, 1936.

Wiseman, J. D. H., and Bennett, H., 1940. The distribution of organic carbon and nitrogen in sediments from the Arabian Sea. John Murray Exp. (1933-34) Sci. Rep., Brit. Mus. Nat. Hist. V. 3, No. 4, 193-221.

*Zimmer, C. L., 1912. Sudwestafrikanische Schizopoda Schultze Zool., Antrop. Ergeb. Forschung Sud-Africa V. 5, pt. 1; Jena Denkschr. Med. Geo. V. 17, 1-11.

Zimmer, C. L., 1914. Schizopoda. Deutsche Sud Polar Exped. 1901-03 V. 15, 377-445.

Zimmer, C. L., 1927. Euphausiacea. In Kukenthal, Handbuch der Zoologie, Leipsig, V. 3, pt. 1, 812-839.

2. Growth.

Anderson, B. G., 1932. The number of pre-adult instars, growth, relative growth, and variation in *Daphnia magna*. Biol. Bull. V. 63, 81-99.

Anderson, B. G., and Busch, H. L., 1941. Allometry in normal and regenerating antennal segments in *Daphnia*. Bull. Biol. V. 81, 119-126.

Anderson, B. G., Lumer, H., and Zupanic, L. J., 1937. Growth and variability in *Daphnia pulex*. Biol. Bull. V. 73, 444-463.

Berrill, N. J., 1941. Spatial and Temporal growth patterns in colonial organisms. Growth, V. 5, 89-111.

Brody, S., 1945. Bioenergetics and growth. Pubn. Herman Frasch Found. (Reinhold Pubn. Cop. N.Y.) 1-1023.

Clark, W. E. le G., and Medawar, P. B., 1945. Essays on Growth and Form presented to Darcy Wentworth Thompson. Clarendon Press, Oxford.

Davidson, J., 1944. On the relationship between temperature and the rate of development of insects at constant temperatures. Jour. Animal Ecol. V. 13, 26-38.

Day, J. H., 1935. Heterogenic Growth in the Abdomen of *Carcinus maenus*. Rep. Dove Mar. Ser. 3, V. 3, 49-59.

Doan, K. H., 1939. Growth of Bass fry. Copeia, No. 2, 81-87.

Dobzhansky and Duncan, 1933. Genes that affect early development stages of *Drosophila melanogaster*. Arch. Entwickl. Mech. Organ. V. 133, 109, 130.

Fowler, G. H., 1909. Biscayan Plankton. Trans. Linn. Soc. Lond. V. 10, pt. 9, ser. 2, 224.

Gray, J., 1929. The Kinetics of Growth. Brit. Jour. Exp. Biol. V. 5, No. 3, 248-274.

Hersh, A. H., 1934. Evolutionary relative growth in the *Titanotheres*. Amer. Nat. V. 68, 537-561.

Hubbs, C. L., and Whitlock, S. C., 1929. Diverse types of young in a single species of fish, the gizzard shad. Pap. Mich. Acad. Sci. Art. Lett. V. 10, 461-482.

Huxley, J., 1932. Problems of Relative Growth. London. Methuen and Co.

Lerner, J. M., 1937. Relative growth and hereditary size limitation in the domestic fowl. Hilgardia V. 10, 511-560.

Lumer, H., 1937. The consequences of sigmoid growth for relative growth functions. Growth, V. 1, 140.

Mottley, C. McC., 1941. The co-variance method of comparing the head lengths of Trout from different environments. Copeia, No. 3, 154.

Needham, A. E., 1937. On relative growth in *Asellus aquaticus*. Proc. Zool. Soc. Lond. Ser. A, V. 107, 289.

Needham, A. E., 1943. On relative growth in *Asellus aquaticus*. Proc. Zool. Soc. Lond. Ser. A, V. 113, 44-75.

Needham, A. E., 1950. The form transformation of the abdomen of the female pea crab, *Pinnotheres pisum* Leach. Proc. Roy. Soc. Ser. B, No. 886, V. 137, 115-136.

Needham, J., 1942. Biochemistry and Morphogenesis. Cambridge University Press, Cambridge, 1-785.

Reeve, E. C. R., 1940. Relative growth in the snout of anteaters. Proc. Zool. Soc. Lond. V. 110, 47-80.

Richards, O. W., 1935. Analysis of the constant differential growth ratio. Carnegie Inst. Wash. Publn. 452, 173-183.

Richards, O. W., 1941. Variation and changes of sign of the relative growth ratio for larval salamander eyes transplanted on starving hosts. Growth, V. 5, 17.

Richards, O. W., and Kavanagh, H. J., 1943. The analysis of the relative growth gradients and changing form of growing organisms illustrated by the tobacco leaf. Amer. Nat. V. 77, 385-399.

Williams, G., and Needham, A. E., 1941. Metric variations in populations of *Carcinus moenas*. Journ. Mar. Biol. Ass. U.K. V. 25, 261-281.

Zuckerman, S., *et al.*, 1950. A discussion on the measurement of growth and form. Proc. Roy. Soc. V. 137, 433-523.

3. Palaeontology.

Peach, B. N., 1908. Monograph on the higher Crustacea in the Carboniferous rocks of Scotland. Mem. Geol. Surv. Gr. Brit. Palaeontology, V. 1, pt. 1, 1-82.

*These papers not sighted.

Printed at The Hassell Press, Adelaide

REPORTS OF B.A.N.Z. ANTARCTIC RESEARCH EXPEDITION, 1929-1931

SERIES B.

		s.	d.
		sterling (post free)	
Vol. IV. Part 1.	Collembola, *by H. Womersley*; Loricata, *by B. C. Cotton*; Brachiopoda, *by B. C. Cotton*; Coleoptera, *by H. Womersley* (1937)	5	0
Part 2.	Cumacea and Nebaliacea, *by H. M. Hale* (1937)	3	6
Part 3.	Diptera, *by H. Womersley*; Miscellaneous Insecta, *by H. Womersley*; Lepidoptera, *by H. Womersley and N. B. Tindale* (1937)	4	6
Part 4.	Polychaeta, *by C. C. A. Monro* (1939)	9	6
Part 5.	Opiliones and Araneae, *by V. V. Hickman* (1939)	4	6
Part 6.	Crinoidea, *by D. Dilwyn John* (1939)	3	6
Part 7.	Endoprocta, *by T. Harvey Johnston and L. Madeline Angel* (1940)	3	6
Part 8.	Nemerteans, *by J. F. G. Wheeler* (1940)	3	6
Part 9.	Decapod Crustacea, *by Herbert M. Hale* (1941)	5	0
Part 10.	Echinoidea, *by Th. Mortensen* (1950)	8	0
Vol. V. Part 1.	Pycnogonida, *by Isabella Gordon* (1944)	10	0
Part 2.	Parasitic Nematodes, *by T. Harvey Johnston and Patricia M. Mawson* (1945).	12	6
Part 3.	Isopoda-Valvifera, *by Herbert M. Hale* (1946)	10	6
Part 4.	Sipunculids, *by A. C. Stephen* (1948)	6	0
Part 5.	The Mollusca of Macquarie Island. Gastropods and Bivalves, *by J. R. Le Tomlin* (1948)		
Part 6.	Foraminifera, *by Walter J. Parr* (1950)	40	0
Vol. VI. Part 1.	Plankton of the Australian Antarctic Quadrant, Part 1, *by Keith Sheard* (1947)	4	6
Part 2.	Isopoda, *by Herbert M. Hale* (1952)	10	0
Vol. VII.	Lichens and Lichen Parasites, *by Carroll W. Dodge* (1948)	60	0
Vol. VIII. Part 1.	Taxonomy, Distribution and Development of the Euphausiacea (Crustacea), *by Keith Sheard* (1952)	32	0

Other Reports are in preparation.